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THE

WILDER

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A COLLECTION OF ORIGINAL PAPERS DEDICATED TO

PROFESSOR BURT GREEN WILDER

AT THE CLOSE OF HIS TWENTY-FIFTH
YEAR OF SERVICE
IN CORNELL UNIVERSITY
(*1868–1893*)

BY

SOME OF HIS FORMER STUDENTS

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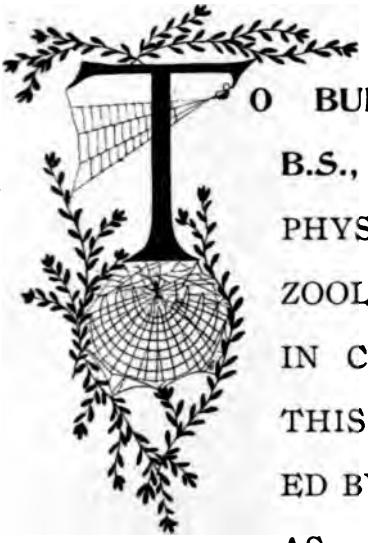

TO **BURT GREEN WILDER, B.S., M.D.,** PROFESSOR OF PHYSIOLOGY, VERTEBRATE ZOOLOGY, AND NEUROLOGY IN CORNELL UNIVERSITY, THIS VOLUME IS DEDICATED BY HIS FORMER PUPILS, AS A TESTIMONIAL OF THEIR APPRECIATION OF HIS UNSELFISH DEVOTION TO THE UNIVERSITY, AND IN GRATEFUL REMEMBRANCE OF THE INSPIRATION OF HIS TEACHING AND EXAMPLE.

TABLE OF CONTENTS

AND OF CONTRIBUTORS.

PAGE.

PORTRAIT OF PROFESSOR BURT GREEN WILDER. Engraved by John P. Davis, *Secretary of the Society of American Wood-Engravers* . . . . . Frontispiece.

LIST of the more important scientific publications of Professor Wilder 1

TABLE showing the number of students taught by Professor Wilder 9

DAVID STARR JORDAN, LL.D., *President of the Leland Stanford Junior University.* Temperature and Vertebræ—A Study in Evolution, Being a Discussion of the Relations of the Numbers of Vertebræ among Fishes to the Temperature of the Water and to the Character of the Struggle for Existence 13

ANNA (BOTSFORD) COMSTOCK, B.S., *Member of the Society of American Wood-Engravers, Natural History Artist.* I. Engraving of a Cat (following page 36). II. Engravings of Moths (Plate I, illustrating the Essay on Evolution and Taxonomy).

JOHN HENRY COMSTOCK, B.S., *Professor of Entomology and General Invertebrate Zoology in Cornell University, and Professor of Entomology in The Leland Stanford Junior University.* Evolution and Taxonomy. An Essay on the Application of the Theory of Natural Selection in the Classification of Animals and Plants, Illustrated by a Study of the Evolution of the Wings of Insects, and by a Contribution to the Classification of the Lepidoptera, (with three plates, and thirty-three figures in the text) 37

EUGENE ROLLIN CORSON, B.S., M.D., *Physician and Surgeon, Savannah, Ga.* The Vital Equation of the Colored Race and its Future in the United States 115

LELAND O. HOWARD, M.S., *First Assistant Entomologist, U. S. Department of Agriculture, Washington, D. C.* The Correlation of Structure and Host-Relation among the Encyrtinæ . 177

THEOBALD SMITH, Ph.B., M.D., *Chief of the Division of Animal Pathology, Bureau of Animal Industry, U. S. Department of Agriculture, Professor of Bacteriology and Hygiene in the Medical Department of the Columbian University, Washington, D. C.* The Fermentation Tube with Special Reference to Anaerobiosis and Gas Production among Bacteria, (with one plate) 187

WILLIAM CHRISTOPHER KRAUSS, B.S., M.D., *Physician, Professor of Pathology, Medical Department of Niagara University, Buffalo, N. Y.* Muscular Atrophy Considered as a Symptom, (with one plate and three figures in the text) 235

SUSANNA PHELPS GAGE, Ph.B. The Brain of Diemyctylus viridescens, from Larval to Adult Life, and Comparisons with the Brain of Amia and of Petromyzon, (with eight plates) 259

HERMANN MICHAEL BIGGS, A.M., M.D., *Professor Materia Medica, Therapeutics, and Nervous Diseases, Bellevue Hospital Medical College, Visiting Physician and Pathologist, Bellevue Hospital, Neurologist and Pathologist to the Hospital of the Work House and Alms House, Chief Inspector Div. Path. Bact. and Disinfection, N. Y. City Health Department.* A Bacterial Study of Acute Cerebral and Cerebro-Spinal Lepto-Meningitis 315

JOHN CASPER BRANNER, Ph.D., *Professor of Geology in the Leland Stanford Junior University.* Observations upon the Erosion in the Hydrographic Basin of the Arkansas River above Little Rock 325

VERANUS ALVA MOORE, B.S., M.D., *First Assistant in the Division of Animal Pathology, Bureau of Animal Industry, U. S. Department of Agriculture, Assistant Demonstrator of Pathological Histology in the Medical Department of the Columbian University, Washington, D. C.* The Character of the Flagella on the Bacillus Choleræ Suis (Salmon and Smith), Bacillus Coli Communis (Escherich), and the Bacillus Typhi Abdominalis (Eberth), (with one plate) 339

GRANT SHERMAN HOPKINS, D.Sc., *Instructor in Anatomy, Microscopy, and Embryology in Cornell University.* The Lymphatics and Enteric Epithelium of Amia calva, (with two plates) 367

PIERRE AUGUSTINE FISH, B.S., *Instructor in Physiology, Vertebrate Zoology, and Neurology in Cornell University, and Instructor in Zoology, Marine Biological Laboratory at Wood's Holl.* Brain Preservation, with a Résumé of some Old and New Methods, (with one plate) 385

WILLIAM RUSSELL DUDLEY, M.S., *Professor of Botany in the Leland Stanford Junior University.* The Genus Phyllospadix, (with two plates) 403

SIMON HENRY GAGE, B.S., *Associate Professor of Anatomy, Histology, and Embryology in Cornell University.* The Lake and Brook Lampreys of New York, Especially those of Cayuga and Seneca Lakes, (with eight plates) 421

MILTON JOSIAH ROBERTS, M.D., *late Orthopedic Surgeon, New York City.* Flashlight Photography in Surgery and Medicine. (Dr. Roberts's contribution, left incomplete by his death, could not be printed in this volume.)

LIST OF THE MORE IMPORTANT SCIENTIFIC PUBLICATIONS OF BURT GREEN WILDER, B.S., M.D., PROFESSOR OF PHYSIOLOGY, VERTEBRATE ZOOLOGY AND NEUROLOGY IN CORNELL UNIVERSITY.

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Meninges. (The envelopes or membranes of the brain and spinal cord). *Same.* pp. 606–616; 11 fig.

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Besides the publications recorded above Professor Wilder has written many articles on natural history subjects for Harper's Magazine, Atlantic Monthly, Galaxy, Our Young Folks, the New York Tribune, etc. He has also written critical reviews of many scientific works for The Nation and for scientific periodicals.

TABLE SHOWING THE COURSES GIVEN BY PROFESSOR WILDER, WITH THE NUMBER OF STUDENTS PERSONALLY TAUGHT BY HIM DURING EACH COLLEGE YEAR FROM THE BEGINNING OF THE UNIVERSITY, (1868), TO THE TWENTY-FIFTH COMMENCEMENT, (1893).

College Year.	Physiology.	Zoology.	Neurology.	Lab. & Spec. Lect. Courses
1868–69	209	42		
1869–70	230	74		64
1870–71	196	20		21
1871–72	175	36		14
1872–73	156	21		17
1873–74	147	133		37
1874–75	109	73		37
1875–76	144	77	20	47
1876–77	167	101	15	70
1877–78	57		11	55
1878–79	87	72	8	45
1879–80	97	80	16	63
1880–81	92	64	16	103
1881–82	61	37	10	64
1882–83	49	50	4	35
1883–84	64	69	8	40
1884–85	53	42	8	66
1885–86	83	60	9	55
1886–87	130	42	9	14
1887–88	148	37	15	27
1888–89	179	49	23	39
1889–90	170	41	22	40
1890–91	149	39	15	45
1891–92	147	36	23	18
1892–93	162	43	24	22
Totals, . .	3261	1338	256	1038

It is shown by the above table that the total number of students personally instructed by Professor Wilder in *Physiology* during his 25 years in Cornell University is 3,261, in *Zoology*, 1,338, in *Vertebrate Neurology* 256, and the number in special and laboratory courses was 1,038. As physiology is required of all students working in the department of Physiology and

Vertebrate Zoology, the number taking physiology represents the total number of different students taught.

In zoology and neurology the totals represent different individuals, but as they had previously taken physiology they are represented in the total for physiology. As special and laboratory work extends throughout the year and may be taken more than one year, the total in the last column represents more or less duplication. Probably about 450 different students have taken laboratory work, and special courses.

Since 1885–86 the courses in *Anatomical* and *Microscopical Methods*, *Histology* and *Embryology*, while under the general direction of Professor Wilder, were not personally conducted by him, hence the students taking those courses are not included in the table.

Under laboratory and special lecture courses, are included lectures and laboratory work in comparative anatomy, collecting, preserving and mounting specimens, museum methods, systematic zoological work, practical anatomy, embryology, vertebrate homologies, and philosophical anatomy.

From the beginning the general courses of Physiology and Zoology have been abundantly illustrated by lecture-room experiments and the exhibition of specimens and preparations as well as by special demonstrations; but in 1880–81 in Zoology, and 1886–87 in Physiology, in addition to the experiments and demonstrations given by Professor Wilder, he introduced for these large and general classes practical laboratory work, or "*Practicums*," as he designated the work. That is, two thirds of the time devoted to the study was given to lectures and one third to the laboratory work in which the students were trained in gaining knowledge by actual personal investigation.

Until 1888–89 Physiology included also Hygiene, and Zoology included both Vertebrates and Invertebrates until 1876–77. Since that time Dr. Wilder's course in zoology has been exclusively vertebrate. In 1870–71 a course in "*Comparative Neurology*" was given, but it was not until 1875–76 that *Vertebrate Neurology* became an established course. It was called by different names in different years, as "comparative

anatomy of the nervous system of vertebrates," "comparative anatomy of the brain," and "morphology of the brain." It is in this course of neurology perhaps more than in any other that is realized the picture drawn by Agassiz, in his address at the inauguration of the university, of the teacher going before his class with his own thoughts and as an elder brother inspiring his pupils to the most enthusiastic and earnest effort.

TEMPERATURE AND VERTEBRÆ—A STUDY IN EVOLUTION.

BEING A DISCUSSION OF THE RELATIONS OF THE NUMBERS OF VERTEBRÆ AMONG FISHES, TO THE TEMPERATURE OF THE WATER AND TO THE CHARACTER OF THE STRUGGLE FOR EXISTENCE.

By DAVID STARR JORDAN.

The present paper is an attempt to find a relation of cause and effect in connection with the fact that in many groups of fishes the species which live in the warmest water have the fewest vertebræ. As here given, it is a modified reprint, with some additional matter, of a paper entitled "Relations of Temperature to Vertebræ among Fishes," published by the author in Volume XIV of the Proceedings of the U. S. National Museum for 1891, pages 107 to 120.

STATEMENT OF THE PROBLEM.

It has been known for many years that in certain groups of fishes the northern or cold-water representatives have a larger number of vertebræ than those members which are found in tropical regions. To this generalization, first formulated by Dr. Gill in 1863 and applied by him to the *Labridæ*, we may add certain others which have been more or less fully appreciated by ichthyologists, but which for the most part received their first formal statement from the writer in 1891. In groups containing fresh-water and marine members, the fresh-water forms have in general more vertebræ than those found in the sea. The fishes inhabiting the depths of the sea have more vertebræ than their relatives living near the shore. In free-swimming pelagic fishes the number of vertebræ is also greater than in the related shore fishes of the same regions. The fishes of the earlier geological periods have for the most part numerous vertebræ, and those fishes with the low numbers (24 to 26) found in the specialized spiny-rayed fishes appear only in comparatively recent times. In the same connection we

may also bear in mind the fact that those types of fishes (soft-rayed and anacanthine) which are properly characterized by increased numbers of vertebræ predominate in the fresh waters, the deep seas, and in arctic and antarctic regions. On the other hand the spiny-rayed* fishes are in the tropics largely in the majority.

In this paper, I wish to consider these generalizations and the extent to which each is true. I propose to refer all of them to the same group of causes. In fact all of them may be combined into one statement, that in general all other fishes have a large number of vertebræ as compared with the shore-fishes of the tropics. The cause of the reduction in number of the vertebræ must therefore be sought in conditions peculiar to the tropical seas. If in any case an increase in the number of

* For the purpose of the present discussion, we may regard the ordinary fishes, exclusive of sharks, ganoids, eels, and other primitive or aberrant types as forming three categories: (1) The soft-rayed or Physostomous fishes, with no true spines in the fins, with an open duct to the air-bladder, the ventral fins abdominal (the pelvis being attached only by the flesh and remote from the shoulder-girdle), cycloid scales, etc. (2) The spiny-rayed or Acanthopterygian fishes, having usually spines in the dorsal and other fins, no duct to the air-bladder, the skeleton firm, the ventrals attached by the pelvis to the shoulder-girdle, the shoulder-girdle joined to the skull, and the scales usually ctenoid or otherwise peculiar. The vertebræ among spiny-rayed fishes are larger, and therefore generally fewer in number, and their appendages (shoulder-girdle, gill arches, ribs, interspinal bones, etc.,) are more specialized. The spiny-rayed fishes are usually regarded as the most specialized or "highest" in the scale of development. The question of whether, on the whole, they are "higher" or "lower" as compared with sharks and other primitive types is ambiguous, because various ideas are associated with these words "high" and "low." It is certain, however, that the spiny-rayed fishes deviate farthest from the primitive stock, and that the qualities that distinguish fishes as a group are most intensified. In other words, it is in the spiny-rayed fishes that the process of "ichthyization" or fish-forming has gone farthest. A third category would comprise the Anacanthines (cods, flounders, etc.), fishes anatomically similar to the spiny-rayed forms, but without spines to their fins, with weaker skeletons and smaller and more numerous vertebræ. They are "degenerate" or more "generalized" offshoots from the spiny-rayed types, as the eels are from some soft-rayed type.

segments has come about through degeneration, the cause of such degeneration must be sought for in the colder seas, in the rivers and in the oceanic abysses. What have these in common that the sandy shores, rocky islands and coral reefs of the tropics have not?

STATEMENT OF THEORY.

For the purpose of this discussion we may assume the derivation of species by means of the various influences and processes, for which, without special analysis, we may use the term "natural selection."

By the influence of natural selection, the spiny-rayed fish, so characteristic of the present geological era, has diverged from its soft-rayed ancestry.

The influences which have produced the spiny-rayed fish have been most active in the tropical seas. It is there that "natural selection" is most potent, so far as fishes are concerned. The influence of cold, darkness, monotony, and restriction is to limit the direct struggle for existence, and therefore to limit the resultant changes. In general the external conditions most favorable to fish life are to be found in the tropical seas, among rocks and along the coral reefs near the shore. Here is the center of competition. From conditions otherwise favorable to be found in arctic regions, the majority of competitors are excluded by their inability to bear the cold. In the tropics is found the greatest variety in surroundings, and therefore the greatest variety in the possible adjustments of series of individuals to correspond with these surroundings.

The struggle for existence in the tropics is a struggle between fish and fish, and among the individuals of a very great number of species each one acquiring its own peculiar points of advantage. No form is excluded from competition. No competitor is handicapped by loss of strength on account of cold, darkness, foul water, or any condition adverse to fish life. Very few fishes are excluded from the tropical seas by the heat of the water. The land heat of the tropics is often unfavorable to life and especially to activity. But in the sea the temperature is never unfavorable to self activity. The water is never sultry, nor laden with malaria.

The influences which serve as a whole to make a fish more intensely and compactly a fish, and which tend to rid it of every character and every organ not needed in fish life, should be most effective along the rocks and shores of the tropics.

For this process of intensification of fish-like characters, which finds its culmination in certain specialized spiny rayed* fishes of the coral reefs, we may conveniently use the term "*Ichthyization*"

If "ichthyization" is in some degree a result of conditions found in the tropics, we may expect to find a less degree of specialization in the restricted and often unfavorable conditions which prevail in the fresh waters, in the cold and exclusion of the polar seas, and especially in the monotony, darkness, and cold of the oceanic abysses where light cannot penetrate and where the temperature scarcely rises above the freezing point.

An important factor in "ichthyization" is the reduction of the number of segments or vertebræ, and a proportionate increase in the size and complexity of the individual segment and its appendages.

If the causes producing this change are still in operation, we should naturally expect that in cold water, deep water, dark water, the fresh waters, and in the waters of a past geological epoch the process would be less complete and the numbers of vertebræ would be larger, while the individual vertebræ remain smaller, less specialized and often imperfectly ossified. And this, in a general way, is precisely what we find in the examination of skeletons of a large series of fishes.

If this view is correct, we have a possible theory of the reduction in numbers of vertebræ as we approach the equator. It should, moreover, not surprise us to encounter various modifications and exceptions, for we know little of the habits and scarcely anything of the past history of great numbers of species. The present characters of species may depend on occurrences in the past concerning which even guesses are impossible.

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* The Parrot-fishes (*Scaridæ*), Trigger-fishes (*Balistidæ*), Angel-fishes (*Chætodontidæ*), etc.

In considering the increase in number and corresponding reduction in size of the vertebræ of northern fishes, it is often very difficult to distinguish between primitive simplicity, such as the salmon and herring show, and the lack of complexity which may be due to "Panmixia" or the cessation of selection—examples of which may be found in the *Liparididæ* and perhaps in the cod and arctic blennies.

We have also, in connection with the process of ichthyization, something of what Professor Dana calls "*Cephalization.*" Features of this are (1) the attachment of the shoulder-girdle to the skull, which occurs in most recent fishes, but which is carried to co-ossification in the case of some of the most specialized, (*Balistidæ*, *Tetrodontidæ*, etc.). (2) The attachment of the pelvis to the shoulder-girdle or to the head, shown in the spiny-rayed fishes and their allies, and (3) the modification and specialization of various bones of the jaws and gill arches, which is in the most specialized forms often accompanied by co-ossification or by reduction in number of the bones concerned. Connected with these changes is the gradual reduction or loss of the air-bladder, which is a degenerate lung, doubtless used for air-breathing by the ganoid ancestors of the modern fishes. In the spiny-rayed fishes it is a closed sac, often so small as to be functionless and very often it is wholly absent.

NUMBERS OF VERTEBRÆ.

We may now consider in detail the numbers of the vertebræ in the different groups of fishes:

Lancelets.—In the different species of *Branchiostoma* or lancelet, a group which stands at the bottom of the vertebrate series, probably diverging from the fish-stock before the formation of a brain or organs of special sense, the number of segments is large, from 50 to 80.

Lampreys.—In the lampreys and hag-fishes, low and to some extent primitive types, which show no trace of limbs or jaws, the vertebræ are cartilaginous and numerous, being little specialized. The number in species examined is more than a hundred, the range being perhaps from 100 to 150.

The fin rays of the vertical fins are little developed and very numerous, both being primitive characters.

The Sharks.—The sharks and skates show likewise a very large number of vertebræ, 120 to 150 in the species in which they have been counted. In these fishes no comparative study of the vertebræ has been made. The group is a very ancient one in geological time, and in the comparatively few remaining members of the group, the vertebræ, in fact the entire skeleton, is in a very primitive condition, the vertebræ being cartilaginous, the fin rays slender and very numerous, not provided with separate interspinal bones. The sharks are free-swimming fishes, and with them as with the eels, flexibility of body is essential to the life they lead.

One of the living sharks, *Chlamydoselachus*, said to be the oldest living type of vertebrate, has the body greatly elongate, fairly eel-shaped, and it doubtless has a maximum number of vertebræ. A large number of cartilaginous vertebræ is also found in the group of *Chimæras*, and in the *Dipnoi*, a very ancient type allied to the ganoids, and doubtless the parent stock of the batrachians and through these of the reptiles, birds, and mammals. Among the batrachians a reduction in the number of vertebræ is associated with the abandonment of aquatic life.

Ganoid Fishes.—It may be taken for granted that the ancestry of the various modern types of bony fishes is to be sought among the ganoids. All the fossil forms in this group have a notably large number of vertebræ. The few now living are nearly all fresh-water fishes, and among these, so far as known, the numbers range from 65 to 110.*

Soft-rayed Fishes.—Among the *Teleostei* or bony fishes, those which first appear in geological history are the *Isospondyli*, the allies of the salmon and herring. These have all numerous vertebræ, small in size, and none of them in any notable degree modified † or specialized. In the northern seas *Isospondyli* still exceed all other fishes in number of

* Sixty-seven in *Polypterus*, 110 in *Calamoichthys*, 95 in *Amia*, etc.

† As is indicated by the name *Isospondyli*, from ἴσος, equal, σπόνδυλος, vertebra.

individuals. They abound in the depths of the ocean, but there are comparatively few of them in the tropics.

The *Salmonidæ** which inhabit the rivers and lakes of the northern zones have from 60 to 65 vertebræ. The *Scopelidæ*, *Stomiatidæ*, and other deep-sea analogues have from 40 upwards to perhaps 100, in the few species in which the number has been counted. In these the weakness of the skeleton and the frequent disconnection of the shoulder girdle from the head seem to be features of degradation.

The group of *Clupeidæ* † is probably nearer the primitive stock of *Isospondyli* than the salmon are. This group is essentially northern in its distribution, but a considerable number of its members are found within the tropics. The common herring ‡ ranges farther into the arctic regions than any other. Its vertebræ are 56 in number. In the shad, § a northern species which ascends the rivers, the same number has been recorded.

The sprat || and sardine ¶ ranging farther south, have from 48 to 50, while in certain small herring ** which are strictly confined to tropical shores the number is but 40.

Allied to the herring are the anchovies, mostly tropical. The northernmost species,†† the common anchovy of Europe, has 46 vertebræ. A similar species in the temperate Pacific (*Stolephorus mordax*) has 44. A tropical species ‡‡ has 41 segments.

There are, however, a few soft-rayed fishes §§ confined to the tropical seas in which the numbers of vertebræ are still large, an exception to the general rule for which there is no evident reason unless it be connected with the wide distribution of these almost cosmopolitan fishes, which may have had pelagic ancestors.

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* Salmon, trout, grayling, whitefish, etc.

† Herring, shad, sprat, sardine, and their allies.

‡ *Clupea harengus*.

§ *Clupea alosa*, the European shad.

|| *Clupea sprattus*.

¶ *Clupea pilchardus*.

** *Harengula macrophthalma*.

†† *Engranlis enchrasicolus*.

‡‡ *Stolephorus browni*.

§§ Among these are *Albula vulpes*, the bonefish, with 70 vertebræ, *Elops saurus*, the ten-pounder, with 72, the Grande Écaille (*Megalops*) with 57, and *Chanos chanos* with 72.

In a fossil herring-like fish from the Green River shales, I count 40 vertebræ; in a bass-like or serranoid fish from the same locality 24, these being the usual numbers in the present tropical members of these groups.

The *Plectospondyli* are those soft-rayed fishes in which the four anterior vertebræ are highly modified, co-ossified and having a peculiar relation to the organ of hearing. The *Siluridæ*, *Cyprinidæ*, *Catostomidæ*, *Characinidæ*, *Gymnotidæ*, and *Electrophoridæ* with their relatives belong here. This peculiar structure of the vertebræ is found in no other group. It could hardly have arisen independently in the different families, hence these great groups including the vast majority of fresh-water fishes must be referred to a common stock.

The great family of *Siluridæ* or catfishes seems to be not allied to the *Isospondyli*, but a separate offshoot from another ganoid type allied to the sturgeons. This group is represented in all the fresh waters of temperate and tropical America, as well as in the warmer parts of the Old World. One division of the family, containing numerous species, abounds on the sandy shores of the tropical seas. The others are all fresh-water fishes. So far as the vertebræ in the *Siluridæ* have been examined, no conclusions can be drawn. The vertebræ in the marine species range from 35* to 50; in the North American forms from 37 to 45,† and in the South American fresh water species, where there is almost every imaginable variation in form and structure, the numbers range from 28 to 50 or more.

The *Cyprinidæ*,‡ also belonging to the group of *Plectospondyli*, confined to the fresh waters of the northern hemisphere, and their analogues, the *Characinidæ* of the rivers of South America and Africa, have also numerous vertebræ, 36 to 50 in most cases. I fail to detect in either group any relation in these numbers to surrounding conditions. The related *Gymnotidæ* and *Electrophoridæ* of the tropical rivers have many vertebræ.

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* *Tachysurus*, *Felichthys*, etc.

† *Ictalurus*, *Ameiurus*, etc.

‡ Carp, minnows, suckers, chubs, buffalo-fishes, gudgeons, etc.

In general, we may say of the soft-rayed fishes that very few of them are inhabitants of tropical shores. Of these few, some, which are closely related to northern forms, have fewer vertebræ than their cold-water analogues. In the northern species, the fresh-water species and the species found in the deep sea, the number of vertebræ is always large, but the same is true of some of the tropical species also.

Spiny-rayed Fishes.—Among the spiny-rayed fishes, the facts are more striking. Of these, numerous familes are chiefly or wholly confined to the tropics, and in the great majority of all the species the number of vertebræ is constantly 24,* 10 in the body and 14 in the tail (10+14).

In some families in which the process of ichthyization has gone on to an extreme degree, as in certain plectognath fishes,† there has been a still further reduction, the lowest number, 14, existing in the short inflexible body of the trunkfish,‡ in which the vertebral joints are movable only in the base of the tail. In all these forms, the process of reduction of vertebræ has been accompanied by specialization in

* This is true of all or nearly all the *Serranidæ*, *Sparidæ*, *Sciænidæ*, *Chætodontidæ*, *Hæmulidæ*, *Gerridæ*, *Gobiidæ*, *Acanthuridæ*, *Mugilidæ*, *Sphyrænidæ*, *Mullidæ*, *Pomacentridæ*, etc.

† *Balistes*, the trigger fish, 17; *Monacanthus* and *Alutera*, foolfishes, about 20; the trunkfish, *Ostracion*, 14; the puffers, *Tetraodon* and *Spheroides*, 18; *Canthigaster*, 17; and the headfish, *Mola*, 17. Among the *Pediculates*, *Malthe* and *Antennarius* have 17 to 19 vertebræ, while in their near relatives, the anglers, *Lophiidæ*, the number varies with the latitude. Thus, in the northern angler, *Lophius piscatorius*, which is never found south of Cape Hatteras, there are 30 vertebræ, while in a similar species, inhabiting both shores of the tropical Pacific, *Lophiomus setigerus*, the vertebræ are but 19. Yet, in external appearance, these two fishes are almost identical. It is, however, a notable fact that some of the deep-water *Pediculates*, or angling fishes, have the body very short and the number of vertebræ correspondingly reduced. *Dibranchus atlanticus*, from a depth of 3,600 fathoms, or more than 4 miles, has but 18 vertebræ, and others of its relatives in deep waters show also small numbers. These soft-bodied fishes are simply animated mouths, with a feeble osseous structure, and they are perhaps recent offshoots from some stock which has extended its range from muddy bottom or from floating seaweed to the depths of the sea.

‡ *Ostracion.*

other respects. The range of distribution of these fishes is chiefly though not quite wholly confined to the tropics.

A very few spiny-rayed families are wholly confined to the northern seas. One of the most notable of these is the family of viviparous surf fishes,* of which numerous species abound on the coasts of California extending to Oregon, and Japan, but which enter neither the waters of the frigid nor the torrid zone. These fishes seem to be remotely connected with the *Labridæ*† of the tropics, but no immediate proofs of their origin exist. The surf fishes have from 32 to 42 vertebræ, numbers which are never found among tropical fishes of similar appearance or relationship.

The fact of variation in the numbers of vetebræ was first noticed among the *Labridæ*. Here the facts are most striking. In the genera of *Labridæ* inhabiting northern Europe and the New England waters (*Labrus*, *Acantholabrus*, *Ctenolabrus*, *Tautoga*,) there are 38 to 41 vertebræ, in the Mediterranean forms (*Symphodus*, etc.,) 30 to 33, in certain semi-tropical genera (*Lachnolaimus*, *Harpe*, *Trochocopus*) 27 to 29, while in those genera which chiefly abound about the coral reefs (*Scarus*, *Sparisoma*, *Xyrichthys*, *Julis*, *Thalassoma*, *Halichœres*) the number is from 23 to 25.

Equally striking are the facts in the great group of *Cataphracti*, or mailed-cheek fishes, a tribe now divided into several families, diverging from each other in various respects, but agreeing in certain peculiarities of the skeleton.‡

Among these fishes the family most nearly related to ordinary fishes is that of the *Scorpænidæ*.§

This is a large family containing many species, fishes of local habits, swarming about the rocks at moderate depths in all zones. The species of the tropical genera have all 24 vertebræ.|| Those genera chiefly found in cooler waters, as in

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* *Embiotocidæ*.

† Wrasse fishes, old wives, parrot fishes, cunners, tautogs, redfishes, señoritas, etc.

‡ Notably by the formation of a bony "stay" to the preopercle by the backward extension of one of the suborbital bones.

§ Sea scorpions, rockfishes, "rock cod," rosefishes, etc.

|| *Scorpæna*, *Sebastoplus*, *Pterois*, *Synanceia*, *Synancidium*, etc.

California,* Japan, Chili, and the Cape of Good Hope, have in all their species 27 vertebræ, while in the single arctic genus there are 31.† An antarctic genus‡ bearing some relation to *Sebastes* has 39.

Allied to the *Scorpænidæ*, but confined to the tropical or semi-tropical seas, are the *Platycephalidæ*, with 27 vertebræ, and the *Cephalacanthidæ* with but 22. In the deeper waters of the tropics are the *Peristediidæ*, with 33 vertebræ, and extending farther north, belonging as much to the temperate as to the torrid zone, is the large family of the *Triglidæ*,§ in which the vertebræ range from 25 to 38.

The family of *Agonidæ*,‖ with 36 to 40 vertebræ, is still more decidedly northern in its distribution. Wholly confined to northern waters is the great family of the *Cottidæ*,¶ in which the vertebræ ascend from 30 to 50. Entirely polar and often in deep waters are the *Liparidiidæ*,** an offshoot from the *Cottidæ*, with soft, limp bodies, and the vertebræ 35 to 65. In these northern forms there are no scales, the spines in the fins have practically disappeared, and only the anatomy shows that they belong to the group of spiny-rayed fishes. In the *Cyclopteridæ*,†† likewise largely arctic, the body becomes short and thick, the backbone inflexible, and the vertebræ are again reduced to 28. In most cases, as the number of vertebræ increases, the body becomes proportionally elongate. As a result of this, the fishes of arctic waters are, for the most part, long and slender, and not a few of them approach the form of eels. In the tropics, however, while elongate fishes are common enough, most of them (always excepting the eels) have the normal number of vertebræ, the greater length being due

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* *Sebastichthys* and its offshoots *Sebastodes*, *Sebastopsis*, etc., the "rock cod" of California. † The rosefish, *Sebastes* and its offshoot, the genus or subgenus, *Sebastolobus*. ‡ *Agriopus*

§ The gurnards and sea robins. The lowest numbers are found in the American genus *Prionotus*, which is chiefly tropical, the highest in *Lepidotrigla*, which is confined to southern Europe.

‖ Sea poachers, alligator fishes, etc. ¶ Sculpins, Miller's thumbs, etc.

** Sea snails. †† Lumpfishes,

to the elongation* of their individual vertebræ and not to their increase in number.

In the great group of blenny-like fishes the facts are equally striking. The arctic species are very slender in form as compared with the tropical blennies, and this fact, caused by a great increase in the number of their vertebræ, has led to the separation of the group into several families. The tropical forms composing the family of *Blenniidæ*† have from 28 to 49 vertebræ, while in the arctic genera the numbers range from 75 to 100.

The anacanthine fishes in whole or in part seem to have sprung from a blennioid stock. Of these the most specialized group is that of the flounders,‡ below described. The wide distribution of this family, its members being found on the sandy shores of all zones, renders it especially important in the present discussion. The other anacanthine families are chiefly confined to the cold waters or to the depths of the seas.

In the cod family§ (*Gadidæ*) the number of vertebræ is usually about 50, and in their deep-sea allies, the grenadiers|| or rat-tails, the numbers range from 65 to 80.

*Thus the very slender goby, *Gobius oceanicus* has the same number (25) of vertebræ as its thick-set relative *Gobius soporator* or the chubby *Lophogobius cyprinoides*.

†Of the true *Blenniidæ*, which are all tropical or semi-tropical, *Blennius* has 28 to 35 vertebræ; *Salarias*, 35 to 38; *Labrosomus*, 34; *Clinus*, 49; *Cristiceps*, 40. A fresh water species of *Cristiceps* found in Australia has 46. Blennioid fishes in the Arctic seas are *Anarrhichas*, with 76 vertebræ; *Anarrhichthys*, with 100 or more; *Lumpenus*, 79; *Muræenoides*, 85; *Lycodes*, 112; *Gymnelis*, 93. *Lycodes* and *Gymnelis* have lost all the dorsal spines and are intermediate between the blennies and the forms called *Anacanthine*. The gradual degeneration of such northern forms may perhaps be attributed to the influence of "Panmixia" or the cessation of selection. ‡*Pleuronectidæ*

§Fifty-one in the codfish (*Gadus callarias*.) 58 in the Siberian cod (*Eleginus navaga*) 54 in the haddock (*Melanogrammus æglifinus*) 54 in the whiting (*Merlangus merlangus*), 54 in the coal-fish (*Pollachius virens*) 52 in the Alaskan coal-fish (*Pollachius chalcogrammus*), 51 in the hake (*Merluccius merluccius*). In the burbot (*Lota lota*) the only fresh water codfish, 59; in the deep water ling (*Molva molva*), 64; in the rocklings (*Gaidropsarus*) 47 to 49. Those few species found in the Mediterranean and the Gulf of Mexico have fewer fin rays and probably fewer vertebræ than the others, but none of the family enter warm water, the southern species living at greater depths. ||*Macruridæ*.

In the family of flounders or *Pleuronectidæ*, a group of wide distribution and in which the individual vertebræ are numerous and little specialized the results are especially striking.

In each of the four principal groups, the numbers agree closely with the geographical distribution of the different genera. Thus in the comparatively primitive subfamily of *Hippoglossinæ*, the halibut group, the division nearest the cod-like stock from which the flounders are probably descended, the numbers range from 35 to 50. In the turbot group (*Psettinæ*) from 31 to 43. In the plaice group, (*Pleuronectinæ*) 35 to 65. In the sole group, (*Soleinæ*) 28 to 49. The tongue-fishes (*Cynoglossinæ*) are elongate like the eels, and specialized in analogous ways. Although all tropical, the numbers counted range from 47 to 52.*

Fresh Water Fishes.—Of the families confined strictly to the fresh waters the great majority are among the soft-rayed or

*These facts may be shown in tabular form as follows:

HIPPOGLOSSINÆ.

Hippoglossus, 50, Arctic.
Atheresthes, 49, Arctic.
Hippoglossoides, 45, Subarctic.
Lyopsetta, 45, Subarctic.
Eopsetta, 43, Subarctic.

PSETTINÆ.

Monolene, 43, Deep Sea.
Lepidorhombus, 41, Arctic.
Orchopsetta, 40, Subarctic.
Platophrys, 37 to 39, Tropical.
Arnoglossus, 38, Semitropical.
Zeugopterus, 37, Temperate.
Bothus, 36 Temperate.
Syacium, 35 to 36, Tropical.
Citharichthys, 34 to 36, Tropical.
Phrynorhombus, 35, Semitropical.
Etropus, 34, Tropical.
Azevia, 33, Tropical.
Psetta, 31, Tropical.
Psettichthys, 40, Subarctic.
Paralichthys, 35 to 41, Temperate and Semitropical.
Xystreurys, 37, Semitropical.
Ancylopsetta, 35, Semitropical.

PLEURONECTINÆ.

Glyptocephalus, 58 to 65, Arctic and deep sea.
Microstomus, 48 to 52, Arctic and deep sea.
Parophrys, 44, Subarctic.
Pleuronectes, 43, Subartctic.
Isopsetta, 42, Subarctic.
Lepidopsetta, 40, Subarctic.
Limanda, 40, Subarctic.
Liopsetta, 40 Subarctic.
Pleuronichthys, 38 to 40, Temperate.
Flesus, 36, Temperate.
Pseudopleuronectes, 36, Temperare.
Hypsopsetta, 35, Semitropical.
Platichthys, 35, Subarctic.

physostomous fishes, the allies of the salmon,* pike, carp, and cat-fish. In all of these the vertebræ are numerous. A few fresh water families have their affinities entirely with the more specialized forms of the tropical seas. Of these the *Centrarchidæ* (comprising the American fresh-water sun-fish† and black bass ‡) have on the average about 30 vertebræ, the pirate perch § 29, and the perch || family, perch and darters, etc., 35 to 45, while the *Serranidæ* or sea bass, the nearest marine relatives of all these, have constantly 24. The marine family of demoiselles¶ have 26 vertebræ, while 30 to 40 vertebræ usually exist in their fresh-water analogues (or possibly descendants), the *Cichlidæ*, of the rivers of South America and Africa. The sticklebacks,** a family of spiny fishes, confined to the rivers and seas of the north, have from 31 vertebræ to 41. The *Ophiocephalidæ*, *Anabantidæ* and other old world families of fresh water fishes have more vertebræ than their marine analogues. No fresh water fishes (except a few *Sciænidæ*,†† which have come comparatively recently into fresh waters) have the number of vertebræ as low as 24, the usual number in the spiny-rayed shore fishes of the tropics.

Pelagic Fishes.—It is apparently true that among the free swimming, or migratory pelagic fishes, the number of vertebræ is greater than among their relatives of local habits. This fact is most evident among the scombriform fishes, the allies of the mackerel and tunny. All of these belong properly to the warm seas, and the reduction of the vertebræ in certain forms has no evident relation to the temperature, though it seems to be related in some degree to the habits of the species. Perhaps the retention of many segments is connected with that strength and swiftness in the water for which the mackerels are preëminent.

The variations in the number of vertebræ in this group led Dr. Günther, nearly 30 years ago, to divide it into two families, the *Carangidæ* and *Scombridæ*.

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* *Cyprinidæ*, *Salmonidæ*, *Esocidæ*, *Characinidæ*, *Cyprinodontidæ*, *Siluridæ*, etc.

† *Lepomis.* ¶ *Pomacentridæ.* || *Percidæ.*

§ *Aphredoderidæ.* ‡ *Micropterus.* ** *Gasterosteidæ.*

†† *Aplodinotus Plagioscion Pachyurus*, etc.

The *Carangidæ** are tropical shore fishes, local or migratory to a slight degree. All these have from 24 to 26 vertebræ. In their pelagic relatives, the dolphins,† there are from 30 to 33; in the opahs,‡ 45; in the *Brama*, 42; while the great mackerel family,§ all of whose members are more or less pelagic, have from 31 to 50.

Other mackerel-like fishes are the cutlass|| fishes, which approach the eels in form and in the reduction of the fins. In these the vertebræ are correspondingly numerous, the numbers ranging from 100 to 160.

In apparent contradistinction to this rule, however, the pelagic family of swordfishes,¶ remotely allied to the mackerels, and with even greater powers of swimming, has the vertebræ in normal number, the common swordfish having but 24.

The Eels.—The eels constitute a peculiar group of uncertain, but probably soft-rayed, ancestry, in which everything else has been subordinated to muscularity and flexibility of body. The fins, girdles, gill arches, scales, and membrane bones are all imperfectly developed or wanting. The eel is perhaps as far from the primitive stock as the most highly "ichthyized" fishes, but its progress has been of another character. The eel would be regarded in the ordinary sense as a degenerate type, for its bony structure is greatly simplified as compared with its ancestral forms, but in its eel-like qualities it is, however, greatly specialized. All the eels have vertebræ in great numbers. As the great majority of the species are tropical, and as the vertebræ in very few of the deep-sea forms have been counted, no conclusions can be drawn as to the relation of their vertebræ to the temperature.

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*Pampanos, amber fishes, pilot fishes, cavallas, etc.

† *Coryphæna.* ‡ *Lampris.*

§ *Scombridæ.* The mackerel (*Scomber scombrus*) has 31 vertebræ; the chub mackerel (*Scomber colias*), 31; the tunny (*Albacora thynnus*), 39; the long-finned albacore (*Albacora alalonga*), 40; the bonito (*Sarda sarda*), 50; the Spanish mackerel (*Scomberomorus maculatus*), 45.

|| *Trichiuridæ: Aphanopus*, 101 vertebræ; *Lepidopus*, 112; *Trichurus*, 159.

¶ *Xiphiidæ.*

It is evident that the two families most decidedly tropical in their distribution, the morays* and the snake eels,† have diverged farthest from the primitive stock. They are most "degenerate," as shown by the reduction of their skeleton. At the same time they are also most decidedly "eel-like," and in some respects, as in coloration, dentition, muscular development, most highly specialized. It is evident that the presence of numerous vertebral joints is essential to the suppleness of body which is the eel's chief source of power.

So far as known the numbers of vertebræ in eels range from 115 to 225, some of the deep-sea eels‡ having probably higher numbers, if we can draw inferences from their slender or whip-like forms; but this character may be elusive.

VARIATIONS IN FIN-RAYS.

In some families the number of rays in the dorsal and anal fins is dependent on the number of vertebræ. It is therefore subject to the same fluctuations.§ This relation is not strictly proportionate, for often a variable number of rays with their interspinal processes will be interposed between a pair of vertebræ. The myotomes or muscular bands on the sides are usually coincident with the number of vertebræ. As, however, these and other characters are dependent on differences in vertebral segmentation, they bear the same relations to temperature that the vertebræ themselves sustain.

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* *Murænidæ.* Among the morays, *Muræna helena* has 140; *Gymnothorax meleagris*, 120; *G. undulatus*, 130; *G. moringa*, 145; *G. concolor*, 136; *Echidna catenata*, 116; *E. nebulosa*, 142; *E. zebra*, 135. In other families the true eel, *Anguilla anguilla*, has 115; the Conger eel, *Leptocephalus conger*, 156; *Muræsox cinereus*, 154; *M. coniceps*, 154; *Ophichthys ocellatus*, 134; *O. gomesi*, 141; *Synaphobranchus pinnatus*, 146; *Gordiichthys irretitus*, 225.

† *Ophisuridæ.*

‡ *Nemichthys, Nettastoma, Venefica.*

§ Thus in the *Scorpænidæ*, *Sebastes*, the arctic genus has the dorsal rays XV, 13, the vertebræ 12 + 19. The tropical genera *Scorpæna* and *Sebastoplus* have the dorsal rays XII, 10, the vertebræ 10 + 14, while the semitropical genus *Sebastodes* has the intermediate numbers of dorsal rays XII, 12, and vertebræ 12 + 15.

CONCLUSION.

From the foregoing examples we may conclude that, other things being equal, the numbers of vertebræ are lowest in the shore-fishes of the tropics, and especially in those of local habits, living about rocks and coral reefs.

The cause of this is to be found in the fact that in these localities the influences of natural selection are most active. The reduction of vertebræ may be regarded as a phase in the process of specialization which has brought about the typical spiny-rayed fish.

These influences are most active in the warm, clear waters of tropical shores, because these regions offer conditions most favorable to fish life, and to the life of the greatest variety of fishes. No fish is excluded from competition. There is the greatest variety of competitors, the greatest variety of fish-food, and the greatest variety of conditions to which adaptation is possible. The number of species visiting any single area is vastly greater in the tropics than in cold regions.

A single drawing of the net on the shores of Cuba* will obtain more different kinds of fish than can be found on the coasts of Maine in a year. Cold, monotony, darkness, isolation, foul water; all these are characters opposed to the formation of variety in fish life. The absence of these is a chief feature of life in the tropical waters.

The life of the tropics, so far as the fishes are concerned, offers analogies to the life of cities, viewed from the standpoint of human development. In the same way the other regions under consideration are, if we may so speak, a sort of ichthyological backwoods. In the cities, in general, the conditions of individual existence are most easy, but the competition is most severe. The struggle for existence is not a struggle with the forces and conditions of nature. It is not a struggle with wild beasts, unbroken forests, or a stubborn soil, but a competition between man and man for the opportunity of living.

* In 1884 a single haul of a net in a shallow bay on Key West brought in seventy-five species of shore-fishes. A week's work about Martha's Vineyard yielded but forty-eight kinds.

It is in the cities where the influences which tend to the modernization and concentration of the characters of the species, that the intensification of human powers and their adaptation to the various special conditions go on most rapidly. That this intensification is not necessarily progress either physical or moral is aside from our present purpose.

It is in the cities where those characters and qualities not directly useful in the struggle for existence are first lost or atrophied.

Conversely it is in the "backwoods," the region most distinct from human conflicts, where primitive customs, antiquated peculiarities, and useless traits are longest and most persistently retained. The life of the backwoods will be not less active and vigorous, but it will lack specialization.

It is not well to push this analogy too far, but we may perhaps find in it a suggestion as to the development of the eels. In every city there is a class which partakes in no degree of the general line of development. Its members are specialized in a wholly different way, thereby taking to themselves a field which the others have abandoned, and making up in low cunning what they lack in strength and intelligence.

Thus among the fishes we have in the regions of closest competition a degenerate and non-ichthyized form, lurking in holes among rocks and creeping in the sand, thieves and scavengers among fishes.

The eels fill a place which would otherwise be left unfilled. In their way, they are perfectly adapted to the lives they lead. A multiplicity of vertebral joints is useless to the typical fish, but to the eel strength and suppleness are everything, and no armature of fin or scale or bone so desirable as its power of escaping through the smallest opening.

It may be too that, as rovers in the open sea, the strong, swift members of the mackerel family find a positive advantage in the possession of many vertebræ, and that to some adaptation to their mode of life we must attribute their lack of "ichthyization" of the skeleton. But this is wholly hypothetical, and we may leave the subject with the general conclusion that with the typical fish advance in structure has

specialized the vertebræ, increased their size and the complexity of their appendages, while decreasing their number. That with some exceptions and modifications this reduction is characteristic of fishes in the tropics, and that it is so because in the tropics the processes of evolution are most active, so far as the fishes are concerned.

UNEXPECTED VARIABILITY IN THE NUMBER OF SEGMENTS.

The most surprising feature in the present investigation is that the number of segments in the adult animal should be determined so late in the process of evolution and that it should be so easily affected by the reaction from differences in external conditions. There are several cases of species almost alike in external characters, differing one from the other in the number of vertebræ, this difference being associated with the distance of the range of the species from the tropics. There are numerous cases in which such marked differences distinguish species which no one would think of placing in different genera (in *Siphostoma*, for example).

In other cases (*Sebastes*, *Sebastodes* and *Sebastoplus*; *Lophius* and *Lophiomus*) genera commonly recognized are distinguishable only by their numbers of vertebræ. This fact shows that the character in question is a recent one, arising after all general matters of form, coloration and appearance have become fixed. That the less number of vertebræ might characterize tropical families as a whole as compared with less specialized extra-tropical groups is not strange. That its influence should be felt within the range of almost every widely distributed family or even genus, and in some cases even within the limits of a species, is certainly surprising.

MATTERS FOR FURTHER INVESTIGATION.

This matter has been thus far studied only in the skeletons of adult fishes. It should be extended to their embryology, that we may find out whether in fishes with 24 vertebræ a larger number is present in the young. If so, we should know by what process the segments disappear.

We should know also in each group which are the ancestral or primitive forms. We should know whether the arctic members of any group are those primitively of many segments, or whether their characters are due to degradation through "Panmixia," or from other cause. This investigation should be extended to each group, and the answers in different groups may be different.

The analogy of the reduction in number and the specialization of the individual vertebræ and fin-rays, to the reduction and specialization of wing-veins in Lepidoptera, as shown by Professor Comstock should be studied. The resemblance of the results of evolution in Fishes and Insects indicate a likeness in the causes.

The correlated changes in the brain and nervous system should also be studied. Mr. Frank Cramer has suggested to me that the process of "Ichthyization" should have given tropical forms larger and more specialized cephalic ganglia. To this end, the size and form of brain in *Sebastes*, *Sebastodes* and *Scorpæna* should be carefully studied. Similar studies in the *Labridæ*, *Pleuronectidæ*, *Blenniidæ* and *Lophiidæ* ought to yield interesting results.

It will be also interesting to know whether any analogous changes have taken place in any other groups of animals as Snakes, Lizards, Batrachians, Crabs, Centipedes or Insects. But among land-animals it will not be surprising if the results are different for the conditions are not quite parallel. With fishes the greatest tropical heat of sea-water is never too great for comfort, nor is it often greater than the natural temperature of the fish. The heat of the land is often much greater than this and it may be so great as to interfere with individual growth of land animals, and it may thus check competition instead of stimulating it.

In any event, a comparative study of the relations of segments to temperature in any group cannot fail to yield interesting results.

HISTORICAL SKETCH.

Günther, 1862.—The earliest observation on record in reference to the subject in question was made by Dr. Albert Gün-

ther. He noted that among the *Labridæ*, the species of temperate waters had more vertebræ than those of the tropics. He says :*

In those genera of *Labridæ* which are composed entirely or for the greater part of tropical species the vertebral column is composed of twenty-four vertebræ, whilst those which are chiefly confined to the temperate seas of the northern and southern hemispheres have that number increased in the abdominal and caudal portions.

Gill, 1863.—Shortly after, in a review of Dr. Günther's work on the Labroids,† Dr. Theodore Gill showed that this generalization was not confined to the labroids alone, but that "it may also be extended to other families. * * * This generalization is applicable to the representatives of acanthopterygian‡ families generally, and can be considered in connection with the predominance of true malacopterygian§ fishes in northern waters, fishes in which the increase in the number of vertebræ is a normal feature."

Gill, 1864.—Later,|| Dr. Gill remarked that the increase in the number of vertebræ of *Sebastes*, a genus peculiar to the northern seas, affords an excellent example of the truth of the generalization claiming an increased number of vertebræ for the cold-water representatives of acanthopterygians.

Jordan, 1886.—In 1886, in a paper before the Indiana Academy of Sciences,¶ the present writer showed that in very many families the number of veterbræ decreases as we approach the tropics. So constant is this relation that it was thought that it might almost be termed a law. The writer could however suggest no adequate cause by the operation of which such changes are brought about.

Jordan and Goss, 1889.—In a study of the flounders, in 1889,** a table was given showing the numbers of vertebræ in

* Catalogue of the Fishes of the British Museum, vol. IV, p. 65.

† On the Labroids of the Western Coast of North America, Proc. Ac. Nat. Sc., Phila., 1863, p. 221.

‡ Spiny-rayed.

§ Soft-rayed ; here including the anacanthine fishes.

|| Proceedings Academy Natural Science, Phila., 1864, 147.

¶ Still unpublished.

** A Review of the Flounders and Soles (*Pleuronectidæ*) of America and Europe, by David S. Jordan and David K. Goss.

the different species. From this table it was made evident that in that group of flounders,* which includes the halibut and its relatives, the arctic genera † have from 49 to 50 vertebræ. The northern genera ‡ have from 43 to 45, the members of a large semi-tropical genus § of wide range have 35 to 41, while the tropical forms || have from 35 to 37.

In the group of turbots ¶ and whiffs none of the species really belong to the northern fauna, and the range in numbers is from 35 to 43. The highest number, 43,** is found in a deep water species, and the next, 41 and 40,†† in species which extend their range well toward the north.

Among the plaices, which are all ‡‡ northern, the numbers range from 35 to 65, the higher numbers, 52, 58, 65, being found in species §§ which inhabit considerable depths in the arctic seas The lowest numbers |||| (35) belong to shore species which range well to the south.

Concerning this matter, Jordan and Goss remark :

It has already been noticed by Dr. Günther and others that in certain groups of fishes northern representatives have the number of their vertebræ increased. In no group is this more striking than in the flounders.

Gill, 1889.—In a review ¶¶ of the paper above mentioned, Dr. Gill considers in detail the condition of our knowledge of this subject, quoting from the various papers mentioned above and claiming very properly that the first statement of this generalization belonged to himself rather than to Dr. Günther.

Dr. Gill further adds :

The case of the sebastines became still more striking when Messrs. Jordan and Gilbert discovered that the number of vertebræ in the species of *Sebastichthys* and *Sebastodes*, genera intermediate between the northern *Sebastes* and the tropical and subtropical representatives of the family of *Scorpænidæ*, was also intermediate.

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* *Hippoglossinæ*. † *Hippoglossus* and *Atheresthes*.

‡ *Hippoglossoides*, *Lyopsetta*, and *Eopsetta*. § *Paralichthys*.

|| *Xystreurys*, *Ancylopsetta*, etc. ¶ *Psettinæ*.

** *Monolene sessilicauda*. †† *Lepidorhombus whiff-jagonis* and *Citharichthys sordidus*.

‡‡ *Pleuronectinæ*. §§ *Glyptocephalus* and *Microstomus*.

|||| *Platichthys stellatus*, *Hypsopsetta guttulata*.

¶¶ Proceedings of the U. S. National Museum, 1888, p. 604.

But while claiming the generalization that there is a correlation between the increase of vertebræ and the increase of latitude among fishes, I would not assign it an undue value or claim for it the dignity of a law. It is simply the expression of a fact which has no cause for its being now known. It may be added that this generalization is true only in a general sense.

Jordan, 1891.—In another paper* the present writer has said:

This increase in the number of vertebræ in northern forms has been used as a basis of classification of the *Pleuronectidæ* by Jordan and Goss, of the *Scorpænidæ* by Jordan and Gilbert, and it will doubtless prove to have a high value in the subdivision of other families which have representatives in different zones. The cause of this peculiarity of fishes of cold waters is still obscure. Probably the reduction in number of segments is a result of the specialization of structure incident to the sharper competition of the tropical waters, where the outside conditions of life are very favorable for fishes, but the struggle of species against species is most severe.

In this paper is given a table which shows that in the genera of *Labridæ* † inhabiting northern Europe and the New England waters there are 38 to 41 vertebræ, in the Mediterranean forms ‡ 30 to 33, in certain subtropical genera § 27 to 29, while in those *Labroids* which chiefly abound about the coral reefs || the number is from 23 to 25.

Jordan & Eigenmann, 1891.¶—In a recent paper on the *Serranidæ* (sea-bass and groupers) it is stated that the group as a whole belongs to the tropical seas, and that it differs from the related fresh-water family of *Percidæ* by the much smaller number of vertebræ, usually 24, which is the number most common among spiny-rayed fishes. Among the *Serranidæ*, however, two genera form exceptions to the general rule. One of these,** with 35 vertebræ, occurs in the rivers of China, the other,†† with 36 vertebræ, in the mountain streams

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* Review of the Labroid Fishes of America and Europe, p. 2.

† *Labrus, Acantholabrus, Ctenolabrus, Tautoga.*

‡ Chiefly belonging to *Symphodus.* § *Lachnolaimus, Harpe*, etc.

|| *Scarus, Sparisoma, Xyrichthys, Julis, Thalassoma*, etc.

¶ A Review of the Genera and Species of *Serranidæ* found in the waters of America and Europe, by David S. Jordan and Carl H. Eigenmann.

** *Lateolabrax.* †† *Percichthys.*

of Chili and Patagonia. In these two genera the numbers are materially increased, as would be expected if the rule is to hold good. There are, however, other *Serranidæ*, more or less perfectly confined to the fresh waters, and yet retaining the normal number of vertebræ. These are perhaps comparatively recent immigrants from the sea. In evidence of this is the fact that among these forms there is a perfect gradation in habits from the strictly marine,* through migratory† and brackish-water species‡ to those confined to the rivers and lakes.§

Jordan & Fesler, 1893.‖—In a discussion of the sparoid fishes by Jordan & Fesler, reference is made to the fact that the subfamily *Aplodactylinæ* inhabiting the south temperate zone differ from the other *Sparidæ* in the increased numbers of their vertebræ (34 instead of 24) and in the greater numbers of the rays of the dorsal fin. In most other regards, this subfamily closely approaches the subfamily *Girellinæ* of the tropics.

Jordan, 1891.—In a paper entitled "Relations of Temperature to Vertebræ among Fishes," (Proc. U. S. Nat. Mus. 1891. pp. 107–120, I have given a statement of what is known of this subject, this paper serving as a basis for the present treatise.

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* *Dicentrarchus punctatus.* † *Roccus lineatus.*

‡ *Morone americana.* § *Roccus chrysops.*

‖ A Review of the Sparoid Fishes of America and Europe, by David Starr Jordan and Bert Fesler, in the Rept. U. S. Fish. Com. published 1893.

PALO ALTO, CALIFORNIA,
June 15, 1893.

ENGRAVED FOR THE

WILDER QUARTER-CENTURY BOOK,

BY ANNA BOTSFORD COMSTOCK.

COMSTOCK.

PLATE 1.

ENGRAVED FROM NATURE, BY ANNA BOTSFORD COMSTOCK.

EVOLUTION AND TAXONOMY.

AN ESSAY ON THE APPLICATION OF THE THEORY OF NATURAL SELECTION IN THE CLASSIFICATION OF ANIMALS AND PLANTS, ILLUSTRATED BY A STUDY OF THE EVOLUTION OF THE WINGS OF INSECTS, AND BY A CONTRIBUTION TO THE CLASSIFICATION OF THE LEPIDOPTERA.

By JOHN HENRY COMSTOCK.

PART I.

A PROPOSED METHOD STATED.

It is now thirty-four years since the publication of Darwin's Origin of Species; and the great war of opinions which had been imminent for some time, and which broke forth on the appearance of that work, has been fought to a conclusion. There remains no contest except that of a healthy competition in reaping the fruits of the victory. Naturalists differ in their opinions as to details but the great principle of evolution has been firmly established, and our methods of thought have been revolutionized in consequence.

Notwithstanding this I do not believe that the systematists of to-day are making as much use of the theory of descent in taxonomic work as they might. We are still busy describing species as if they were immutable entities; and in our descriptions we give little thought to the causes that have determined the forms of organisms. It is true that considerable has been done in the direction of working out the phylogeny of the larger groups, as branches and classes, and to a less extent of orders. But rarely is any effort made to determine the phylogeny of the smaller groups.

Here I believe lies the work of the systematist of the future. The description of a species, genus, family or order, will be considered incomplete until its phylogeny has been determined so far as is possible with the data at hand. We are to care less for the mere discovery of new forms, and more for an under-

standing of the processes by which new forms have arisen. The object of taxonomy will not be a mere grouping of forms according to similarity of structure. But the systematist will have constantly before him the question: What do these variations of form mean? With this change in the object of taxonomic work, there will come a change in its methods. It is strange that the change has been so long delayed; for we are really using the same methods that were employed before the establishment of the truth of the theory of natural selection. What these methods are was indicated by Darwin in the following words:

"Practically, when naturalists are at work, they do not trouble themselves about the physiological value of the characters which they use in defining a group or in allocating any particular species. If they find a character nearly uniform, and common to a great number of forms, and not common to others, they use it as one of high value; if common to some lesser number, they use it as of subordinate value." (Darwin, Origin of Species, pp. 367–368, Am. Edition.)

This statement is about as true to-day as when Darwin wrote it. For if one will look through the taxonomic works on zoology or botany he will very seldom find any reference to the functions of organs. But almost all naturalists now believe that in each epoch of time the forms of existing organisms have been determined by a survival in preceding generations of those individuals whose parts were best fitted to perform their functions.

Does it not follow from this belief that we can confidently expect to gain much help in our efforts to work out the phylogeny of organisms by making a careful study of the functions of their organs, and endeavoring to understand the reasons for the action of natural selection?

I suggest, therefore, that the logical way to go to work to determine the affinities of the members of a group of organisms is first to endeavor to ascertain the structure of the primitive members of this group; and then endeavor to learn in what ways these primitive forms have been modified by natural selection, keeping in mind that in each generation those

forms have survived whose parts were best fitted to perform their functions.

Obviously there are certain difficulties in the carrying out of this plan. But the measure of our success in determining the affinities of the organisms studied, will depend largely on our ability to overcome these difficulties.

Among the difficulties encountered is the fact that usually our classification must be based largely on a study of living forms; for in most cases the aid to be derived from Palaeontology is comparatively slight. But although the record presented by fossils is very fragmentary, fortunately there are many living forms which are comparatively slightly specialized. And these will serve to give an idea of the stem form of the group.

Thus to carry out the plan suggested, the zoologist or botanist, if he is forced to work only with living animals or plants, will select from the group to be studied the most generalized type before him, and then trace out the different ways in which this type has been modified in the more specialized forms.

If the group studied be a large one, the probabilities are that instead of a single primitive type, several generalized forms will be found, each representing more or less approximately the stem form of a distinct line of development; and a comparative study of these different forms will be necessary in order to obtain an idea of the structure of their common ancestor.

But how shall one go to work to select from a large number of forms those that are to be considered the more generalized? The higher animals and plants are such complex organisms that it is not an easy matter to determine the relative degree of specialization of two distinct forms. The problem is also complicated by the fact that even the more generalized forms may present specializations peculiar to themselves.

Numerous examples will occur to any systematist of forms which as a whole are comparatively generalized, but which in some respects are highly specialized, being, as has been expressed by some writers, "sidewise developed." It is essen-

tial that these sidewise developments be not included in our conception of the still more primitive form.

Thus the Thysanura are regarded as the most generalized of the living Hexapoda. This would also be the case if of this order only the suborder Collembola were known to us. In such a case we might conclude from a study of the spring-tails that the primitive Hexapoda possessed a ventral sucker and a caudal spring, and that these organs had been superceded by the wings in more specialized forms. Now we know that while taken as a whole the Collembola are very generalized insects, that so far as the ventral sucker and caudal spring are concerned they do not represent the primitive type of the order, but are sidewise developed. In both the Cinura and the Collembola we find forms which are clothed with highly specialized scales, scales which rival in complexity of structure those of the Lepidoptera. Yet no one believes that the primitive Hexapoda were so clothed. This is another sidewise development. And the scales of the Lepidoptera, and of the Curculionidæ, for example, have arisen independently.

We thus see that although in our efforts to trace out the series of modifications through which a line of organisms has passed we may find forms which appear primitive, we must not expect to find among living forms an exact record of these changes. Each form studied will represent the tip of a twig which has separated from the main branch. Fortunately for our purpose we can often find some forms representing twigs that branched off very early and that have not grown very far in their special direction. In many cases too, forms are found which although highly specialized as regards some of their organs will retain a generalized condition of other organs. By a comparison of a number of such forms each representing a generalized condition of some of its organs we can get an approximate idea of the common progenitor.

But I repeat, how shall we determine which are the representatives of those short twigs that have undergone but little change, and which are the representatives of branches that have been greatly modified? The answer to this question is

a statement of the method I propose for applying the theory of natural selection to taxonomy more fully than has been done before.

As the structure of a highly organized animal or plant is too complicated to be understood in detail at once, it is suggested that the student begin with the study of a single organ possessed by the members of the group to be classified, and that his studies take the following course: First the variations in form of this organ should be observed, including palæontological evidence if possible; then its function or functions should be determined. With this knowledge endeavor to determine what was the primitive form of the organ and the various ways in which this primitive form has been modified, keeping in mind the relation of the changes in form of the organ to its function. In other words endeavor to read the action of natural selection upon the group of organisms as it is recorded in a single organ. The data thus obtained will aid in making a *provisional* classification of the group.

When this stage has been reached another organ should be selected and its history worked out in a similar way.

The results of the two investigations should then be compared; and where they differ there is indicated the need of renewed study. For if rightly understood the different records of the action of natural selection will not contradict each other. The investigation should be continued by the study of other organs and a correlating of the results obtained until a consistent history of the group has been worked out.

This method differs from that commonly employed in being a constant effort to determine the action of natural selection in the modification of the form of organisms in order to better adapt their parts to preform their function. Ordinarily little or no attention is devoted to the study of the functions of organs in purely taxonomic works.

If the history of a group be worked out in the manner indicated, the student will feel the need of recording his results in such a way as to indicate the phylogeny of the divisions of the group. But as the necessities of book making require a linear arrangement of descriptions this is somewhat difficult; for the

natural sequence of groups should be represented by constantly branching lines rather than by a single straight line.

It seems to me that the most practicable way of meeting this difficulty is to begin with the description of the most generalized form known, and to follow this with descriptions of forms representing a single line of development, passing successively to more and more specialized forms included in this line. When the treatment of one line of development has been completed take up another line beginning with the most generalized member of that line and clearly indicating in the text that a new start has been made.

Much aid can also be given by a tabular statement of the essential characters of the subordinate groups, using the form of the ordinary analytical table. An illustration of this is given in Part III of this essay.

In this connection reference should be made to the proper position of degraded forms in a series where an effort is made to represent the natural sequence. The common practice of assigning such forms the same position that would be assigned to them if their simplicity of structure was the result of a primitive condition seems to me illogical. An example will make this point clear. The Hemiptera are doubtless all descended from a common winged ancestor. The lice, although more simple in structure than most other members of the order, do not represent the form of this ancestor as closely as do the winged members of this order. They should not, therefore, be placed first in the hemipterous series as is commonly done. It would represent the facts of nature better to place them last, as forms departing more widely from the primitive type of the order than do the winged forms. But it should be clearly indicated that although they represent the tip of one of the lines of development that line is a downward bending line.

In attempting to work out the phylogeny of a group of organisms, there will arise, I believe, the necessity of distinguishing between two kinds of characters: first, characters indicating differences in *kind* of specialization; and second, characters indicating differences in *degree of specialization of*

the same kind. The former will indicate dichotomous divisions of lines of descent; the latter will merely indicate degrees of divergence from a primitive type. Thus, to draw an illustration from the following pages, it is shown that there are two distinct ways of uniting the two wings of each side in the Lepidoptera; they may be united by a frenulum (Fig. 22) or the may be united by a jugum (Fig. 27). These are differences in *kind* of specialization, and indicate two distinct lines of descent or a dichotomous division of the order. Among those Lepidoptera in which the wings are united by a frenulum great differences occur in the degree to which this organ or a substitute for it is developed; such differences may merely indicate the degree of divergence from a primitive type and may need to be correlated with other characters to indicate dichotomous divisions.

It is impracticable to indicate degrees of divergence from the primitive type based on the nature of the frenulum at this stage of the discussion; but another character will serve our purpose well. In the more generalized Lepidoptera the anal areas of one or of both pairs of wings are furnished with three anal veins; while in more specialized forms the number may be reduced to two or even to one. But the distinctions indicated by the presence of three, two, and one anal veins in different moths, are merely differences in degree of specialization by reduction of an anal area, and taken alone will not indicate dichotomous divisions. Thus if we group together all the moths that have retained three anal veins in the hind wings, such a group will contain, not merely the Microlepidoptera, as is commonly stated, but also the more generalized members of several distinct divisions of the Macrolepidoptera.

The fact is, the primitive Lepidoptera evidently possessed at least three anal veins in the hind wings (we will omit the fore wings from the discussion for the time being). In several distinct lines of development within this order the direction of specialization of the anal area of the hind wings has been towards the reduction of the number of veins in this area; but the extent to which this reduction has gone merely indicates the degree of divergence from the primitive type. And so far

as this single character is concerned a similar degree of divergence in a similar direction may be possessed by members of widely separated divisions of the order.

But we are not entirely dependent on differences in kind of specialization for indications of dichotomous divisions. Such divisions may be indicated by differences in the order in which specializations take place.

This also can be illustrated by a study of the anal areas of the wings. It is evident that in the primitive Lepidoptera the fore wings as well as the hind wings possessed three anal veins. And in certain divisions of the order the direction of specialization of the anal area of the fore wings has also been towards a reduction in the number of veins. It will be shown in the concluding part of this essay that in certain divisions of the order the reduction of the anal area of the hind wings has preceded the reduction of the anal area of the fore wings; while in other divisions of the order the reverse is the case. Here is an indication of a dichotomus division. Take for example two families of moths, one of which is characterized by the presence of two anal veins in the fore wings and three anal veins in the hind wings; and the other, by three anal veins in the fore wings, and two in the hind wings. In the former, the specialization by reduction of the anal areas has begun in the fore wings; in the latter, this specialization has begun in the hind wings. And it is evident that the common progenitor of the two families had three anal veins in both fore and hind wings, and that the difference in the order in which the reduction of the anal areas has begun indicates a dichotomous division.

There will also arise, I believe, in a work of this kind a necessity for distinguishing between the essential characters of a group and those characters which are used by the systematist merely to enable students to recognize members of the group. For it seems to me that the essential characters of a group of organisms do not lie necessarily in the presence or absence of any structure or structures, or in the form of any part or parts of the body of the living members of the group; but rather in the characteristic structure of the progenitor of

the group, and in the direction of specialization of the descendants of this progenitor.

Thus, to use again the illustration given above, the Jugatæ are essentially characterized as the descendants of those ancient Lepidoptera in which the wings of each side were united by a jugum; and they are also characterized by a tendency towards an equal reduction of the veins of the two pairs of wings. While the Frenatæ are essentially characterized as the descendants of those ancient Lepidoptera in which the wings of each side were united by a frenulum; and they are also characterized by a tendency towards a greater reduction of the veins of the hind wings than of the fore wings, or, in other words, by a tendency towards a cephalization of the powers of flight. The fact that in many of the Frenatæ the frenulum has been lost, does not invalidate in the least the truth of this characterization. The loss of the frenulum, however, in certain Frenatæ renders necessary the use of some other character or characters by the systematists as recognition characters.

The recognition characters are those usually first observed by the investigator, and are those commonly given in taxonomic works. In many cases these recognition characters are also essential characters, especially in the case of groups that have been thoroughly studied. But by the taxonomic methods now commonly used search is chiefly made for recognition characters. The more skilled the systematist the more likely is he to discover and use as recognition characters those that are really essential, although the distinction pointed out here may not be recognized by him.

In the case of those groups where but few or no generalized forms have persisted till this time, the essential characters must to a greater or less extent be inferred. This is especially true of those characters which refer to the structure of the progenitor of the group. But the direction of specialization may be shown by a single representative of the group, if it be highly specialized, and we have a clear idea of the essential characters of a larger group including the one under investigation.

It must be borne in mind, however, that the direction of

specialization may undergo marked changes in the course of the history of a single line of development. Thus I feel sure that in the ancient Frenatæ the tendency of specialization was towards more rapid flight which tendency resulted in the preservation of the narrower winged forms. But while this tendency has been continued in certain divisions of the group to the present time, so that in these divisions the most highly specialized forms have the narrowest wings (Sphingidæ, Zygænina), there are other divisions in which the tendency has been changed towards a different mode of flight, and has resulted in the preservation of the wider winged forms, and in these divisions the most highly specialized forms are those having the widest wings. (Saturniina.)

In recording the results of specialization one is apt to speak as if there were an intelligent directing force which determines the direction of specialization; or as if individuals deliberately chose the way in which they should vary from their progenitors. The fact that we are often able to arrange the members of a group in well defined series, each series culminating in a specialized form towards which the other forms approximate in varying degrees of closeness, leads to the unconscious use of such expressions. It is difficult to keep constantly in mind the extent of the thinning out process that takes place in nature, that the objects of our studies are merely a few fortunate individuals that have withstood tests that have proved fatal to the great majority. Innumerable unfortunate variations perish and leave no record; we see the fortunate ones alone; and the impression is apt to be that there is a definite progression on the part of all. Perhaps the facts of the case can be expressed as follows: The conditions which surround an organism combined with the existing structure of that organism render variations in its offspring in certain definite directions fortunate, while variations in other directions are unfortunate. As the fortunate variations alone are preserved to us the record seems to indicate a strong tendency to vary in definite directions.

In this paper the terms generalized and specialized are used in preference to low and high, which are often loosely used as

synonyms of these terms. It should be remembered that lowness or simplicity of structure may be the result of degradation, and hence does not necessarily indicate a primitive or generalized condition. The lice are the lowest of the Hemiptera; but they are by no means the most generalized of the living members of that order.

Professor Hyatt has pointed out* that specialization may take place in two different ways: first, by an addition or complication of parts, *specialization by addition*; second, by a reduction in the number or in the complexity of parts, *specialization by reduction*. These expressions are very convenient in indicating the direction of specialization of an organ or set of organs.

Another important principle, first pointed out, I believe by Meyrick† is that "When an organ has wholly disappeared in a genus, other genera which originate as offshoots from this genus cannot regain the organ, although they might develop a substitute for it."

The truth of *Meyrick's law*, as this last principle may be termed is obvious when we consider that if a part be wholly lost there is nothing for natural selection to act upon in order to reproduce it. And even if a necessity for the organ should again arise and a substitute be developed for it, it is not at all probable that the substitute would resemble the organ so closely as to be mistaken for it.

In the application of Meyrick's law care must be taken that comparison be made only between allied forms, *i. e.*, within what may be termed a single line of descent. I recognize the fact that these expressions are indefinite, but I believe no systematist will have doubt as to my meaning.

Let me state the matter in another way. The loss of an organ is a character that merely indicates a degree of divergence from a primitive type. And so far as any single organ is concerned this stage may be reached in one line of descent very much earlier than in another. In fact the loss of an organ may be correlated in one line of descent with a very

* *Insecta*, page 51.

† Trans. Lond. Ent. Soc. 1884, page 277.

generalized condition of other characters; while in another line of descent very highly specialized forms may still possess the organ in question.

A good illustration of this is presented by the condition of the mouth in the Macrolepidoptera. In many moths the mouth parts are wanting, while in other moths and in butterflies the maxillae are very highly specialized. It cannot be concluded from this fact that the mouthless forms are farther removed from the primitive type than are the sphinges and butterflies for example. A study of other structures would not support such a conclusion. We have to do in a case of this kind either with very distinct lines of descent or with a sidewise development.

In the case of the organ selected, the mouth, there comes into play, I believe, a very peculiar principle. For a long time I was greatly puzzled by the many instances in which absence of mouth parts is correlated with a very generalized condition of other structures. The explanation of this phenomenon I now believe to be as follows: Under certain conditions natural selection may tend to change the length of the adult stage. In some cases those individuals that most quickly provide for the perpetuation of the species are the ones that are most likely to have offspring. Under such conditions there would be a shortening of the duration of the adult stage until a point was reached at which it would not be necessary for the insect to take food during the adult stage, and the mouth parts would be lost in this stage.

But this shortening of the duration of the adult stage would also tend to a great degree to remove the species that had acquired it from the struggle for existence in this stage. A species that found it necessary to fly only a few hours or even days in order to provide for the perpetuation of its kind would not offer such an opportunity for the action of natural selection upon the structure of its wings and other organs peculiar to the adult, as would surely occur in a species having a longer period of flight.

PART II.

THE EVOLUTION OF THE WINGS OF INSECTS.

This essay is an outgrowth of an effort to determine the phylogeny of the families of the Lepidoptera, in order to decide upon a classification to be used in a general text book of Entomology. More than three years were devoted to the problem before a systematic method of procedure was adopted. This time was largely spent in a comparative study of published classifications and in an effort to determine which of these represented most accurately the facts of nature. A large part of the work yielded poor returns for the labor expended; for it was carried on with no definite plan; it was a blind groping in the dark.

Suddenly one day a flood of light was thrown upon the work by the recognition of the fact that a moth which I was studying (*Hepialis*, Plate I, Fig. 2) was a generalized type. I found that a knowledge of the structure of this insect gave a clue to the probable structure of the primitive Lepidoptera. And that with this knowledge it was not too much to expect to be able to trace out the various lines of descent represented by existing forms. Then began a systematic study which has resulted in the development of the method outlined in Part I of this essay.

I regret that I have been unable to apply the method as fully as I should like to before publishing it. But the results which I have been able to obtain by it lead me to hope that the publication is not premature. And as the leisure which a teacher can get for study is limited, I could not hope to make a complete application of it, even to the families of a single order, for many years.

A complete application of the method to the Lepidoptera alone will involve a study of the segments of the body a sa whole, the peculiarities of development of particular segments, the structure of internal organs, the structure of organs of special sense, the various appendages of the body as antennae, mouth-parts, legs, wings, and the external appendages of the reproductive organs, the clothing of the body, in a word the

study of every structure that has been developed in these insects.

But although this extended study will be necessary before we can consider our work complete, a provisional classification can be based on the study of a single organ or set of organs. We have only to remember that such a classification is merely provisional, and that the results obtained in this way should be confirmed or corrected by the study of other organs.

Following the method indicated, the wings were selected as the first organs to be studied. These organs were chosen as the most available ones, owing to their size, and the ease with which variations in their structure could be observed. The record of the action of natural selection is recorded upon them as upon a broad page. For a long time my attention was confined to the wings of the Lepidoptera. But later I found it necessary to greatly extend my studies in order to determine the primitive type of the wings of insects. It was also necessary to study the wings of insects of other groups in order to select a nomenclature of the wing veins that would apply to all orders of insects.

Although there are great differences in the venation of the wings of insects of different orders, a study of the more generalized members of the several orders of winged insects show that the type of venation is the same for them all. This indicates two points of great scientific interest: first, wings have originated but once in the class Hexapoda, or, to state the same thing in other words, all of the orders of winged insects have descended from a common stock; second, if all the various forms of wings are modifications of the same type, it is not too much to expect to be able to establish a uniform nomenclature for the principal elements in the frame work of the wings, *i. e.*, the principal veins, although doubtless it will be necessary to use special names in many cases for structures that have been developed secondarily.

The importance of the wings of insects for taxonomic purposes was early recognized by entomologists, as is well shown by the fact that the names of the Linnean orders are all drawn from the nature of the wings, except one, *Aptera*, and that from the absence of wings.

Although, doubtless, the great extent to which the wings are still used in taxonomy is partially due to the ease with which wing characters can be observed, still the following considerations show that such use is warranted by the facts of nature.

The chief end of existence of an adult insect is to provide for the perpetuation of the species. This resolves itself in the case of the male into seeking a mate; and in the case of the female after accepting a mate, into seeking a proper nidus for her eggs. In the case of certain insects special conditions necessitate a prolonged existence in the adult state in order to accomplish this end in the best manner; in such cases there may exist a necessity for seeking food; but in many families all nourishment is taken during the adolescent stages.

The necessity for seeking mates or for properly placing eggs, as well as for seeking food gives great importance to organs which increase the power of locomotion. It follows from this that when organs of flight had once been developed such organs would furnish an important field for the action of natural selection.

It has been indicated that there is good reason to believe that all winged insects have descended from a common winged ancestor. But we find that the primitive type of wing has been modified in many widely different ways. Hence a study of the various ways in which wings have been specialized can not fail to throw much light on the phylogeny of insects.

The fact that in some cases, notably those of most animal parasites, wings, becoming unnecessary and perhaps even detrimental, have been lost does not lessen the value of these organs for taxonomic purposes when they have been preserved.

It is often urged, that as the wings are merely appendages of the body, they are extremely liable to be modified in form; and that consequently we cannot hope to find in them a very permanent record. In other words, while it is generally admitted that variations in the framework of the wings may give us important clews as to the limits of the genera, we can not

hope to base conclusions upon them as to the limits of larger groups. But it does not follow, that because an organ is a superficial one, it is of little value in suggesting broad generalizations. We find that often the most superficial of structures are among those that were developed very early in the history of a large group, and have persisted almost unchanged in form, although more central structures have been greatly and variously modified. Thus the form of mere dermal appendages may present characters of very high value, as the hair of mammals and the feathers of birds; even the *Cetacea* have hair, and *Archopteryx* had feathers. As "the proof of a pudding is in the eating," so the value of a character for taxonomic purposes can be determined only by its use.

As to the origin of wings we have no knowledge We have not even a generally accepted theory to account for the appearance of these structures. Many writers believe that they are modified tracheal gills. We find in many aquatic nymphs plate-like gills, some of which would need to be modified but little to function as organs of locomotion. This is especially true of the covering pieces forming part of the respiratory appendages of an Ephemerid nymph. These pieces not only protect the gills beneath them; but probably also serve by their flapping to cause a current of water to pass over the gills. Fig. 1 represents the covering piece of a tracheal gill of an Ephemerid nymph collected at Ithaca. The step from such a structure to one that would aid in locomotion is not a great one.

FIG. 1.–Covering-piece of tracheal gill of May-fly.

But other writers think that the wings arose as keel-like expansions of the sides of the thorax. Such expansions would function as a parachute in a falling insect, as does the folds of skin in a flying squirrel, or would function both as a kite and a parachute in a leaping insect.

In support of the latter theory the netted-veined triangular prolongations at the sides of the prothorax of certain fossil insects (*Chorædodis* and *Lithomantis*, Fig. 2) are brought forward; and it is also said that a species of Tingis from Texas

shows on the prothorax, transparent projections of triangular form and a netted venation similar to that of the fore wings*.

Whatever the origin of wings may have been, I think that this much is clear: they were developed to comparatively large size and were furnished with numerous veins before they began to function as *active* organs of flight. This large size and rich venation may have been the result of a natural selection of those forms best fitted to act as a kite or a parachute. But this type of wing is not well adapted for active flight. As soon as there arose a tendency for the wing to function in this way, there began, doubtless, the extensive series of modifications of which we have records both in the rocks and among living insects.

We know almost as little regarding the origin of the veins of the wings as we do of the wings themselves. Still we may be allowed to speculate regarding the matter. Let us suppose that the wings originated from broadly expanded organs; such organs would be furnished with tracheæ, even if they were used only as a parachute; for they would need to be supplied with air as are other parts of the body. On the modification of such organs into wings fitted for active flight, it would be important that the main trunks of the tracheæ should be protected in such a way that any bending of the wing, which would compress them and thus choke off the supply of air, would be avoided. Thus any tendency of the membrane of the wing to become thickened along the lines of the tracheæ would be preserved by natural selection; and correlated with the development of this firm frame-work, there might be a thinning of the spaces between the main tracheæ, thus insuring lightness of the entire organ.

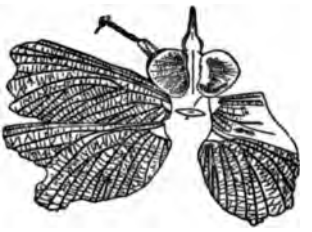

FIG. 2.—*Lithomantis.*

*Josef Rettenbacher, Vergleichende Studien über das Flügelgeäder der Insecten Ann. des k. k. naturhistorischen Hofmuseums, Wien, Bd. I. 153-232, t. IX-XX.

We are not entirely without evidence that this is the method of the formation of wing veins. It will be shown later that when the principal stem of one system of veins (media) is obliterated and the branches of this system are forced to derive their supply of air through lateral tracheæ extending to adjacent systems of veins, these lateral tracheæ become enveloped by veins resembling in every respect the principal veins. Similar evidence may be drawn from the study of the development of the humeral veins in the Lasiocampidæ.

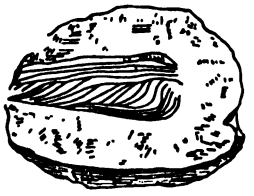

FIG. 3.—*Palæoblattina douvillei.*

Since we are not able to determine the form and function of the organs which were modified into wings, let us endeavor to select the most generalized type of wings preserved to us. We will first see what light Palæontology throws upon this question

Comparatively little is known regarding the primitive insects. But thanks to the labors of Mr. S. H. Scudder, who has been one of the chief workers in this field, what is known has been made easily accessible.*

Winged insects appeared very early, probably as early as any land plants; for Moberg has figured an insect (in the Förhandlingar of the Swedish geological society) from the upper part of the lower silurian; and Brongniart has figured and described a wing from the middle silurian sandstone of Calvados, France. (Fig. 3). But this wing instead of being primitive in form represents a rather highly specialized type, if the figure given correctly represents

FIG. 4.—*Homothetus fossilis.*

* Zittle. Traite de Paleontologie t. II.
Bull. U. S. Geol. Survey No. 31.
Bull. U. S. Geol. Survey No. 69.
Fossil Insects of North America. Vol. I. Pretertiary Insects.
Index to the known Fossil Insects of the World, including Myriapods and Arachnids. Bull. U. S. Geol. Survey No. 71.

its structure. And the insect described by Moberg (*Protocimex silurícus*) is supposed by him to be hemipterous, an even more highly specialized type.

Of devonian insects we know several. Those which are best preserved are *Homothetus fossilis* (Fig. 4), *Xenoneura antiquorum* (Fig. 5), and *Platephemera antiqua* (Fig. 6). These differ among themselves to such an extent that we are forced to conclude without taking into account the two known silurian insects, that already at that early time there was a large and varied insect fauna, of which the more primitive forms have not been discovered.

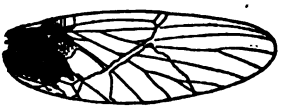

FIG. 5.—*Xenoneura antiquorum.*

From the carboniferous rocks much more abundant material has been obtained. But, according to the views of Mr. Scudder "there existed among these ancient forms no ordinal distinctions, such as obtain to-day, but they formed a single homogeneous group of generalized hexapods, which should be separated from later types more by the lack of those special characteristics which are the property of existing orders than by any definite peculiarity of its own." *

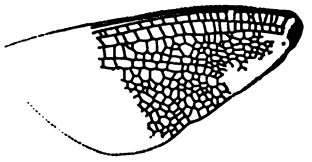

FIG. 6.—*Platephemera antiqua.*

To this group of generalized hexapods which includes all paleozoic insects the name *Palæodictyoptera* has been applied.

Among the Palæodictyoptera were insects which were undoubtedly the precursors of the cockroaches, the may-flies, and the walking-sticks. Still these groups of insects "were more closely related to one another, at least in the structure of their wings (which is the only point of general structure yet open for comparison) than any one of them is to that modern group to which it is most allied." The ordinal distinctions which is now found in the "wing structure of modern insects did not exist in

* Bull. U. S. Geol. Survey. No. 31 p. 104.

paleozoic insects, but a common simple type of venation which barely admitted of family divisions."*

In his classification of the Palæodictyoptera,† Mr. Scudder indicates a number of these family divisions, and groups them according to their general facies and by their relationship to succeeding types into four sections as shown by the following table.‡

PALÆODICTYOPTERA.

ORTHOPTEROIDEA.

1. Fam. *Palæoblattariæ.*
   Subf. *Mylacridæ.*
   Subf. *Blattinariæ.*
2. Fam. *Protophasmidæ.*

NEUROPTEROIDEA.

1. Fam. *Palephemeridæ.*
2. Fam. *Homothetidæ.*
3. Fam. *Palæopterina.*
4. Fam. *Xenoneuridæ.*
5. Fam. *Hemeristina.*
6. Fam. *Gerarina.*

HEMIPTEROIDEA.

Eugereon, Fulgorina, Phthanocoris.

COLEOPTEROIDEA.

Borings supposed to be of beetle-like insects.

It is evident from a study of the fossil remains that our knowledge of the primitive Palæodictyoptera is very fragmentary. The few forms that have been discovered in the silurian and devonian rocks are evidently more highly specialized than certain other forms which have been found in the carboniferous; the most generalized wings known to us, as I shall show later, being from this epoch. We must, therefore, turn to the carboniferous as the earliest epoch from which we have data to base our conclusions regarding the structure of the primitive insect wings.

As this is a comparatively late period we are forced to pursue practically the same method that we would were we to attempt to solve the problem by a study of living insects. That

* Scudder. Pretertiary Insects p. 319, 320.

† Zittle Traite de Paleontologie t. II. and in Bull. U. S. Geol. Survey No. 31.

‡ It would be presumptuous for one who has studied the paleozoic insects so little as I have done to criticise the accepted classification of them. I therefore quote it without change, although it does seem to me that ordinal distinctions arose earlier than indicated by Mr. Scudder.

is we must select what seems to be the more generalized types and try to eliminate from these the results of sidewise developments.

What is gained by the study of carboniferous insects, I believe, is the demonstration that certain characters which have been commonly considered primitive did not exist with these insects, and consequently must be considered as secondary developments.

A comparative study of these insects show that in the Palæodictyoptera the two pairs of wings were very similar in structure both being membranous and furnished with a similar framework of veins.* Each wing possessed six principal veins or groups of veins which are clearly homologous with the *costa*, *subcosta*, *radius*, *media*, *cubitus*, and *anal veins* of modern insects. The wings when not in use were closed over the abdomen. They were sometimes broadly folded but were never plated, as are the hind wings of the Acrididæ for example. This feature being with little doubt a comparatively late development. (See Scudder, *Pretertiary Insects*, p. 49.)

It seems to me probable that the Palephemeridæ presented an exception to the general statement given above, in that the two pairs of wings were not of equal size. The shape of the fore wings of *Platephemera antiqua* (Fig. 6) is such as to indicate that the hind wings were small. And I am informed by Mr. Scudder that the only paleozoic may-fly known that shows the hind wings at all (*Palingenia feistmanteli*) shows that they must have been broad and in all probality much shorter than the fore wings.†

* We find here an intermembral homology analogous to that which exists between the fore and hind limbs of Vertebrates. See an exhaustive paper by Wilder on *Intermembral Homologies*, Proc. Bost. Soc. of Nat. Hist. vol. XIV, p. 154.

†In fact I do not believe that the living May-flies are so primitive as regards their wing structure as has been commonly supposed. They have attained a high degree of cephalization of the function of flight, as shown by the reduction in size of the hind wings, and the large development of the mesothorax. The subcosta and radius are nearly parallel with the costa and closely approximated to it; the wings are well corrugated; and an extensive system of concave veins have been developed. Each of these characteristics is discussed later.

Although the wings of the Palæodictyoptera agree in the characteristics given above they present great differences of structure. How shall we decide which of the different forms is the more primitive. This I think can be done by determining the degree of their adaptation to the performance of their function.

In those insects which have the best developed powers of flight we find that the costal edge of the front wings is the strongest part of the wing, the strength being due to the presence of several strong veins which are nearly parallel. Such an arrangement is necessary to withstand the strain that is brought upon this part of the wing. I conclude, therefore, that wings possessing this structure are more highly specialized than those in which the costal edge is not strengthened in this way. Using this criterion I select that form of wing which departs most widely from this type as the most generalized form ; for so important a character as this when once attained would not be lost so long as the wings were used as organs of vigorous flight. I conclude, therefore, that it is among the carboniferous coachroaches that we find the most generalized form of wing.

Owing to our limited knowledge of extinct forms, I cannot hope to present in these studies continuous series ; but can only select examples which illustrate the direction or directions of specialization of particular parts, without strictly confining myself to a single line of development.

In *Mylacris anthracophilum* (Fig. 7) the wing is furnished with five sets of veins in addition to the costal or marginal vein if this exists. Three of these which occupy the intermediate area of the wing arise each in a single strong trunk. These veins may be designated beginning with the one nearest the costal margin as the *radius*, *media*, and *cubitus*, respectively.

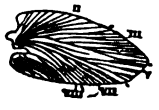

FIG. 7.—*Mylacris anthracophilum.*

Lying between the costal edge of the wing and the radius there is a group of veins which radiate from near the base of the wing (Fig. 7, II). These I believe represent the *subcosta* in its most generalized form.

These subcostal veins resemble very closely in form and arrangement the group of veins lying behind the cubitus, the *anal veins*. In fact a longitudinal line drawn through the center of the wing divides it into two nearly similar halves.

It will be readily seen that this type of wing is poorly fitted for active flight; the costal edge lacking the strength necessary for this purpose. In fact the arrangement of the veins approximates that of the covering piece of a tracheal gill figured above (Fig. 1), or that of the lateral appendages of the prothorax of *Lithomantis* (Fig. 2).

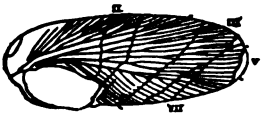

FIG. 8.—*Necymylacris heros.*

In *Necymylacris heros* (Fig. 8, II) we see the beginning of a strengthening of the subcostal area. One of the subcostal veins, the hindermost, becomes the principal vein of this area; and most of the other subcostal veins have become consolidated with this one, so as to appear to be branches of it. The subcostal area is also relatively much narrower.

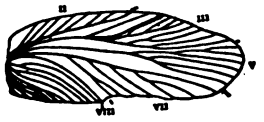

FIG. 9.—*Ectoblattina lesquereuxii.*

In *Ectoblattina lesquereuxii* (Fig. 9) the tendency of the many subcostal veins to become consolidated into a single strong vein with branches extending to the costa is carried much farther; and the narrowing of the subcostal area is also more marked.

The step from the form of the subcosta in *Ectoblattina* to that presented by many modern insects is not a great one, as for example, that of the fore wing of *Corydalis*.

It is probable that correlated with the lengthening and narrowing of the subcostal area in these paleozoic insects a thickening of the costal edge of the wing took place, thus forming the costal vein. As I have been able to study only figures of these paleozoic remains, I am unable to decide at what point in the development of the wing a distinct costal vein was formed. It was probably very early; for Mr. Scudder states that in the paleozoic insects the six principal veins

were always developed, the marginal [costa] simple and forming the costal border.

From this brief study of the development of the subcostal area let us pass to the area lying next to the opposite margin of wing, the anal area, omitting for a time any discussion of the three veins (radius, media and cubitus) which occupy the central portion of the wing.

A striking feature in the structure of the wings of many insects is the separation of the anal area from the remainder of the wing by a fold or furrow, along the bottom of which extends a vein. Such a depressed vein has been termed, on account of its position, a *concave* vein; and in contradistinction to such veins, those veins which extend along the summit of ridges, or which are more prominent on the upper surface of the wing than on the lower, are termed *convex* veins.

This furrow separating the anal area from the preanal portion of the wing appeared very early. It is especially prominent in all cockroaches both fossil and living; and can usually be recognized in any insect wing in which the anal area is well developed. I have been unable to determine the significance of it. But have found it a very useful mark in defining the limits of the anal area. It is vein VIII of the nomemclature adopted in this paper.

The primitive form of the anal area is probably well shown in *Mylacris*, (Fig. 7), where it closely resembles the primitive form of the subcostal area, as shown in the same genus. But the latter specialization of this area has been very different from that of the subcostal. This specialization has taken place in two opposite directions, *i e.*, by reduction and by addition.

In certain lines of development the tendency of natural selection has been to preserve the narrower winged forms. And the narrowing of the wings has taken place largely through a partial or complete reduction of the anal area. The dragon-flies, *Odonata*, and the ant-lions, *Myrmeleon*, are examples of the extreme result of this tendency. And in the Lepidoptera there are several instances where a good series illustrating successive stages in this reduction can be

found. Thus within a single family, or perhaps superfamily, the more generalized members have three anal veins in at least one pair of wings, (usually the hind wings), while as one passes to more and more specialized forms only two, or one anal veins are found.

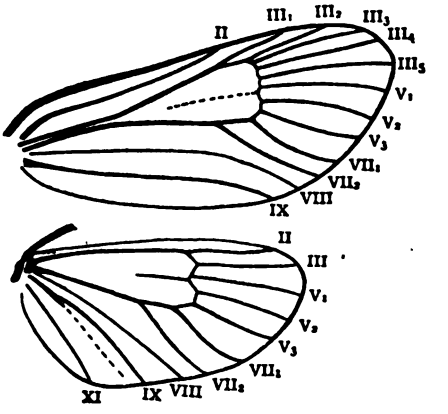

FIG. 10.—*Triprocris.*

I believe that this selection of the narrower winged forms is the result of the survival of those forms that are best fitted for rapid flight. A good illustration of the difference in the powers of flight between an insect with a wide anal area and one in which this area has been reduced, can be found within the limits of a single lepidopterous superfamily, the Zygænina. Compare the power of flight of *Triprocris* (Fig. 10) in which there are two anal veins in the fore wings and three anal veins in the hind wings, with that of *Syntomis* (Fig. 11) in which there is only a single anal vein in both fore and hind wings.

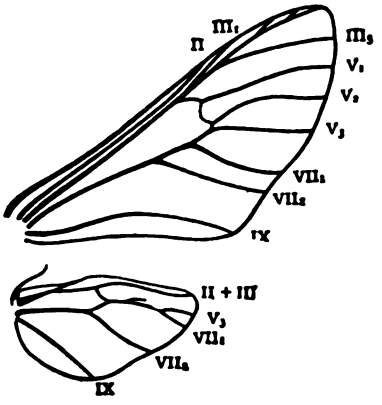

FIG. 11.—*Syntomis.*

On the other hand, in other lines of development, natural selection has evidently tended to a preservation of the wider winged forms; and the widening of the wings has taken place largely by a specialization of the anal area by

addition. The extreme result of this method of specialization is presented by the Orthoptera and especially by the hind wings of the Acrididæ. Here we find a widely expanded anal area, with regularly alternating concave and convex veins. Such a wing is not fitted for striking vigorous and rapid blows upon the air as is required for rapid flight; but is adapted to a sliding flight, a sliding up like a kite or down like a parachute. Such a method of flight would naturally reach its highest development in jumping insects, like the Acrididæ.

A study of the illustrations just given shows that where the tendency of natural selection is towards the development of a rapid flight there is usually a cephalization of the function of flight, *i. e.*, the hind wings are greatly reduced, and the fore wings become the chief organs of flight. This is well shown by the more specialized Zygænids (Fig. 11); and the extreme of such a cephalization is presented by the Diptera. That such a cephalization is not absolutely necessary to rapid flight is shown by the dragon-flies (Odonata); but here the abdomen is greatly elongated, which gives a similar result.

On the other hand where an expansion of an anal area has taken place in order to provide for a sliding flight, it is the hind wings that are specialized by addition, *i. e.*, the opposite of cephalization takes place. The Acrididæ have already been cited as an illustration of this.

The region lying between the subcostal and anal areas is traversed by three principal veins and their branches. These veins as already indicated, are the *radius*, *media* and *cubitus*, the radius lying next to the subcosta, the cubitus next to the anal area, and the media, between the radius and cubitus. Very remarkable modifications take place in the structure of these veins and in their relation to each other. Some of the modifications will be discussed in detail later; in this place I wish only to make some very general statements.

If a large series of wings be examined it will be found that the area of each of these veins may be specialized either by addition or by reduction, *i. e.*, it may be either widened or narrowed. When the tendency of natural selection is to widen one of these areas, the points of origin of the branches

of the principal vein will be nearer the base of the wing in the more specialized forms than in the more generalized members of the same group. On the other hand when the tendency of natural selection is to narrow one of these areas the branches become consolidated with the main stem to a greater and greater distance from the base in the more and more specialized forms. This consolidation of a branch with the main stem or of two branches with each other may extend to the margin of the wing, and thus the number of branches be reduced. This migration of the point of origin of a branch of a

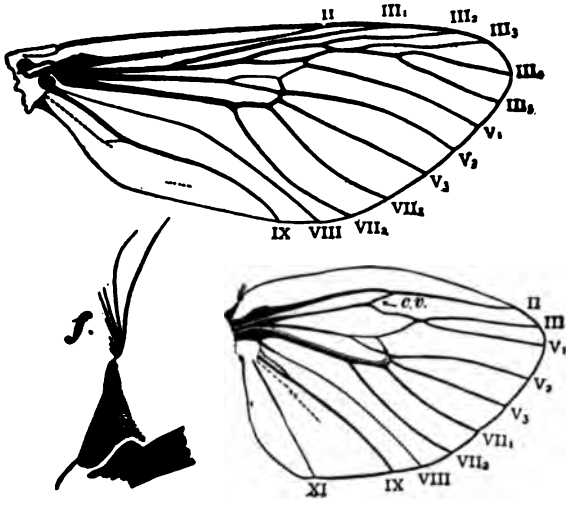

FIG. 12.—*Prionoxystus; f.* frenulum and frenulum brace, enlarged.

vein often affords an excellent clew to the degree of departure from a more generalized type.

But the most remarkable of the changes which take place in this region of the wing is an abortion of the main trunk of media and a consequent uniting of the branches of this vein either with cubitus or with both cubitus and radius. Excellent illustrations of this occur in the Lepidoptera. In many of the more generalized moths the main trunk of media is well preserved (Fig. 12); while in more specialized forms it is en-

tirely wanting. Sometimes, as in *Danais*, remnants of the basal part of the branches of media project back into the discal cell from the discal vein (Fig. 13); while in many other butterflies the branches of media are so completely united with radius and cubitus that there is no indication of the fact that they do not belong to these systems of veins (Fig. 14).

It is probable that in none of the Palæodictyoptera were the wings plaited, as they are in many existing insects; although

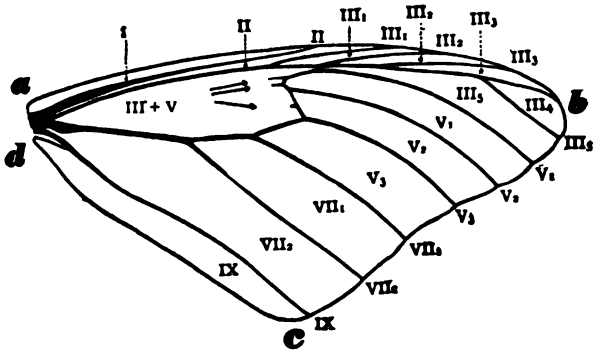

FIG. 13.—Fore wing of *Danais*.

in some, they were broadly folded. And if we except the anal furrow (vein VIII), already referred to, all of the veins were of the type that is termed convex; that is, they were more prominent on the upper surface of the wing than on the lower.

We thus see that the evidence of the Palæodictyoptera does not corroborate the theory of Adolph and Redtenbacher as to the primitive type of the wings of insects. Instead of the primitive wing consisting of regularly alternating concave and convex veins, as described by them, it is probable that the concave veins are a later development, either arising *de novo* or being modified convex veins, excepting always the anal furrow (vein VIII), regarding the origin of which we know nothing.

Concave veins have evidently arisen to meet two distinct needs: first, in those insects in which the wings have become

broadly expanded so as to provide for a sliding flight, there is a necessity for the plaiting of these wings when not in use so that they may be carried without impeding locomotion on foot; second, we find in certain cases where the tendency of specialization has been towards a narrowing of the wings in order to admit of vigorous flight, a corrugation of the wings has taken place in order to strengthen them. The hind wings of a grasshopper illustrate the first; and the wings of a dragon fly present the extreme of the second form of specialization.

It is easy to see that a corrugated wing, like that of the dragon fly, is much stiffer than it would be if the membrane extended in a single plane. If one will examine the cross veins extending between the costa and the radius in a dragon fly, he will find that some of these are in the form of triangular braces which effectually prevent any tendency on the part of the wing to become flattened. Evidently the corrugation is of extreme importance.

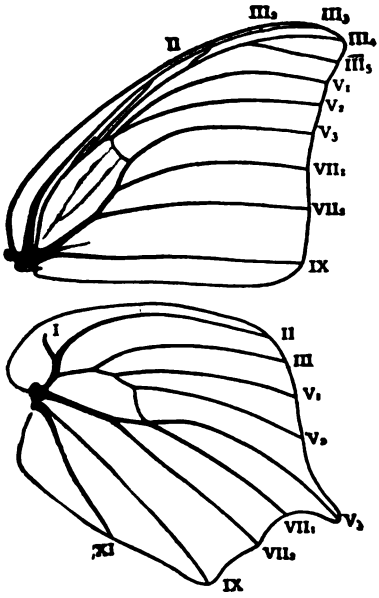

FIG. 14.—*Paphia.*

The concave veins have arisen in two ways. The first of these is by a change in the position of a convex vein. The subcosta in most of the orders of insects is an illustration of this. In the Lepidoptera the subcosta has retained its form as a convex vein, but in most orders of insectst he area between the costa and the radius has been depressed forming a furrow along the bottom of which the subcosta extends. This corrugation has resulted from the need of a stiffening of the costal edge of the wing. The second method of formation of

concave veins is illustrated by a vein that lies between radius and media (vein IV), and also by a vein that lies between media and cubitus (vein VI) in certain orders of insects. These veins (IV and VI) I do not believe existed in the Palæodictyoptera; at least, I have not been able to find any indication of their presence in the figures of paleozoic insects. In the more modern orders of insects when a corrugation of the wings arose, and the areas traversed by these veins became depressed, veins IV and VI appeared. It is probable that they were developed by a straightening out of the zigzag line between two series of cells. This can be readily seen by comparing the wing of one of the devonian may-flies (Plate III, 3) with that of a modern may-fly (Plate III, 5). In the devonian may-fly the cells of the wing are polygonal, while in the modern may-fly they are quadrangular. In the latter case not only have longitudinal concave veins been formed from zigzag lines, but the cross veins extending between these concave veins and the adjacent convex veins have become strictly transverse. An arrangement which insures the preservation of the corrugations.

In a similar way the concave veins in the anal area of the modern Orthoptera have probably arisen.

I conclude, therefore, that in the more highly specialized wings of certain orders of insects, there exists a regular alternation of convex and concave veins, this alternation being the result of a corrugation of the wings for the purpose of stiffening them. This conclusion is quite different than that reached by Redtenbacher, who starts with the fan type of wing as the primitive one.

In the Lepidoptera this corrugation has not taken place, the wings being stiffened by scales, consequently, the subcosta remains a convex vein, and veins IV and VI have not been developed. It is probable that these veins are also lacking in the wings of the Hymenoptera and the Coleoptera, but I have not studied carefully the wings of these insects.

As to the nomenclature of the wing veins of insects, there is no longer any doubt regarding the desirability of a uniform system of naming the veins in the different orders of winged

insects. Only by such a system can those comparisons be made which are necessary in any thorough study of the relationship of the orders to each other. Heretofore the students of each order have had their peculiar nomenclature, and in many cases writers treating of a single family have proposed a set of names to be used in that family alone. The matter has been further complicated by the fact that not only have different names been applied to the same vein, but the same name has been applied to different veins. Thus the terms costa and subcosta have been applied by Lepidopterists to different veins than those that bear these names in other orders.

There have been several attempts to establish a uniform nomenclature. Of these that of Redtenbacher is the most important, being based on a much more extended study of the subject than that made by any other author.

Redtenbacher was the first one to work out a system and apply it to all of the orders of winged insects. And although his system was based on what I believe to be a false theory, and his interpretation of facts in some cases were faulty, I believe that the more essential features of his system can be adopted.

Although, as I have pointed out above, the fan-type of wing was not the primitive type, it seems desirable to base our nomenclature on this type ; for here we find the maximum number of veins ; and our nomenclature should include the secondarily developed veins of modern insects as well as the primitive veins.

I have shown that in the preanal portion of the wing of paleozoic insects there were developed five principal veins. These may be designated, beginning with the one on the costal margin of the wings, as *costa*, *subcosta*, *radius*, *media* and *cubitus*. The term *media* was proposed by Redtenbacher; the others were adopted by him as those sanctioned by the best usage.* I have also shown that in certain insects there

* Redtenbacher was not the first to recognize media as a principal vein. This was done by Edward Doubleday nearly fifty years ago. See his Remarks on the Genus Argynnis, Trans. Linn. Soc. Vol. XIX, 1845. I have adopted the term *media* in preference to *discoidal vein* proposed by Doubleday as the latter might be confused with *discal vein*, the term commonly applied to certain cross veins.

is developed, secondarily, a longitudinal vein between radius and media, for this I propose the term *premedia* ; and also in the same insects there is developed a longitudinal vein between media and cubitus, this I designate as *postmedia*.

Following the system of Redtenbacher these veins may also be designated by Roman numerals. The equivalence of the numbers and names of the veins of the wing is indicated by the following table ; also the nature of the veins.

I.—Costa	convex.
II.—Subcosta, usually	concave, secondarily.
III.—Radius	convex.
IV.—Premedia	concave.
V.—Media	convex.
VI.—Postmedia	concave.
VII.—Cubitus	convex.
VIII.—First anal	concave.
IX.—Second anal . . .	convex.
X.—Third anal	concave,
et al.	

It will be seen from this table that if we consider subcosta a concave vein, which it has come to be in the larger number of the orders of insects, there is a regular alternation of convex and concave veins, when the maximum number of veins is present. And hence the convex veins are designated by odd numerals and the concave veins by even numerals ; this is one of the chief features of Redtenbacher's system, and an exceedingly useful one.

If this system be applied to the anal area, and I believe it is best that it should be, all convex anal veins must be designated by odd numerals. In those orders where the anal area has been greatly specialized by addition, (*e. g.*, Orthoptera), this would naturally follow ; for there we find a regular alternation of concave and convex veins. But in certain other cases it is not so obvious. In those Lepidoptera in which three anal veins are preserved, the first (vein VIII) is concave, and doubtless represents the primitive anal furrow ; the second is convex and is obviously vein IX ; but the third is also convex ! Shall this be designated as vein X, or as vein XI ? It seems to me better that we consider vein X absent,

as are veins IV and VI in this order, and designate this one as vein XI. This view is strengthened by the fact that in many of the Microlepidoptera with broad hind wings there is a prominent fold between the two convex anal veins. This fold may be looked upon as the beginning of an anal vein, which is as yet undeveloped, but which if developed would be vein X.

Another important feature of Redtenbacher's system is the designating of the branches of a vein by Arabic indices appended to the Roman numeral indicating this vein. Thus the branches or radius are designated as III_1, III_2, III_3, etc., (Fig. 15).

While I believe that we are able to trace out homologies between the *principal veins* of the wings of insects of the different orders, I do not think it practicable, even if possible, which I doubt, to homologize the *branches* of the principal veins beyond the limits of a single order. I have not, therefore, adopted in all cases Redtenbacher's plan of using odd indices only for convex branches and even indices only for concave branches. This plan will be found very useful in those orders (*e. g.*, Ephemerida) where the fan-type of wing has been developed; but in other cases (*e. g.*, Lepidoptera) it would merely complicate the nomenclature without ad-

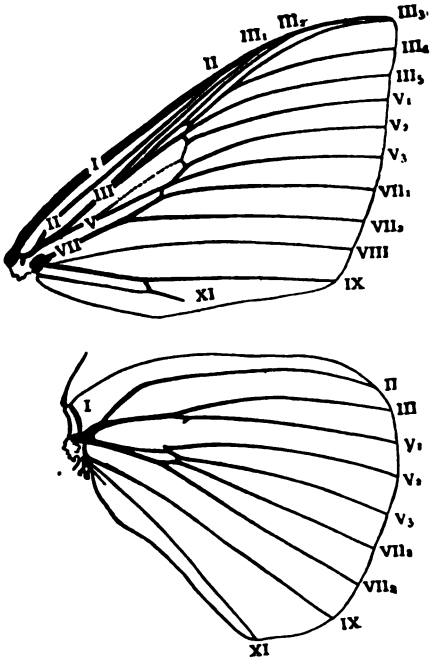

FIG. 15,—*Castnia.*

ding to its value. Thus in the Lepidoptera I designate the five branches of radius as III_1, III_2, III_3, III_4, and III_5 respectively, although all of these branches are convex.

It should be noted that in numbering the branches of a principal vein, they are numbered in the order in which they reach the margin of the wing, not in the order in which they are given off from the main stem. The system adopted is not only the simpler but insures the same number being applied to homologous veins in different genera, which would not be the case were the other system adopted.

Having indicated the more general features in the development of the wings of insects in order to define the nomenclature of the wing veins that I have adopted, and having explained this nomenclature, I can now pass to the consideration of certain details exhibited by the wings of the Lepidoptera.

The more important of these are the changes which take place in media; for this vein in the Lepidoptera is of the highest value for taxonomic purposes.

The tendency to abortion of the main trunk of media has already been pointed out. The explanation of this tendency I have not fully determined satisfactorily to myself, I can only suggest the following: In the course of the narrowing of the wing and the strengthening of the main veins which has taken place as a result of a natural selection of the more active flying forms, the veins have become crowded together at the base of the wing. The more important veins, *i. e.*, radius and cubitus, have held their place, while media has been crowded out. This crowding out has probably taken place in this way. The narrowing of the space occupied by media compressed the large trachea or tracheæ which it contained. Such a compression tends to shut off the supply of air to that part of the wing supplied by the branches of media. To counteract this evil, communication is established between the branch of media and the veins lying on either side of it. When such a communication is well established there is no longer any need for the basal portion of media and it becomes atrophied. In this connection it should be stated that the mem-

brane of the wing is supplied with an immense number of minute tracheæ extending from the main trunks contained in the veins. The lateral branches of the tracheæ are rarely seen even in carefully bleached wings, for in mounting the specimen they become filled with the mounting medium and are thus rendered invisible. But occasionally air will remain in them rendering them distinctly visibly. It is by means of some of these lateral tracheæ that the branches of media become connected with radius and with cubitus.

When such a communication has been established it is important that these tracheæ should not be compressed by the

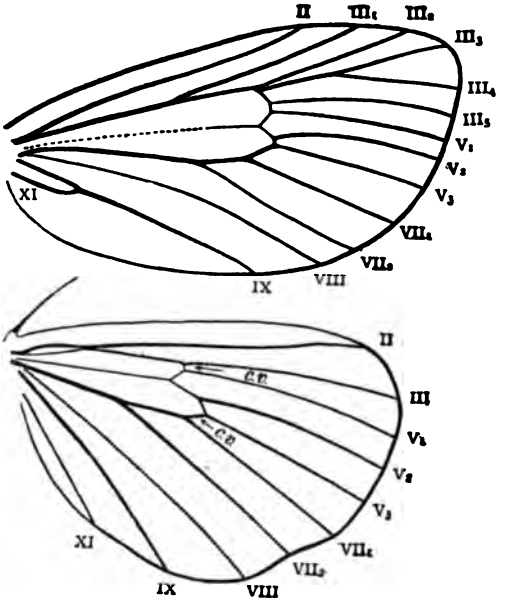

FIG. 16.—*Packardia.*

bending of the wing during flight, therefore any tendency to protect these tracheæ by a thickening of the membrane along their course would be beneficial and would result in the development of veins enclosing these tracheæ.

These veins at first extend in a transverse direction, and are thus obviously cross veins (Fig. 16, *c. v.*). But the result of

farther specialization is to round off the angles in the path of the tracheæ, as the angles in our roads are rounded off by carts. This process is continued until these cross veins become parts of longitudinal veins, and their true nature as cross veins is completely hidden. This is well shown by the connection existing between the third branch of media (vein V_3) and cubitus. A study of the venation of *Castnia* (Fig. 15) shows conclusively that media is three-branched and cubitus only two-branched. Here the connection between vein V_3 and vein VII is obviously a cross vein. But in every American moth and butterfly known to me, except perhaps *Hepialis* and *Micropteryx*, the union of these two veins is so complete that there is no hint of the fact that vein V_3 is not a branch of vein VII. And in several families vein V_2 has also become united with vein VII in a similar manner. The result is that cubitus (the median vein of many authors) is described as three-branched in some families and four-branched in others.

Two years after I had reached the conclusion that media is three-branched and cubitus only two-branched in the Lepidoptera, Spuler published a paper* in which these facts are demonstrated in an entirely different way. As I did not publish my conclusions, the credit of the discovery belongs of course to Spuler. I wish merely to state that my conclusions were reached independently of that author's work, and by an entirely different method. I was led to the correct understanding of the relation of these veins by a study of existing generalized forms (especially *Hepialis* and *Castnia*); while Spuler's conclusions were based on a study of the ontogeny of certain butterflies. He found that in newly formed pupæ the trachea which later becomes enclosed by media is three-branched, while that one which is the precursor of cubitus, is only two-branched. This is an interesting instance of the evidence of ontogeny confirming results obtained in an effort to determine the phylogeny of a group by the study of generalized forms.

* A Spuler.—Zur Phylogenie und Ontogenie des Flügelgeäders der Schmetterlinge. Zeit. fur wissenschaftliche Zoologie, LIII.

Let us see how the facts regarding the changes of media can be used in taxonomic work.

First, the presence of the main trunk of media is an indication of a generalized condition. This at once throws light on the position of the Megalopygidæ, the Psychidæ, the Cossidæ, the Limacodidæ, and certain of the Zygaenina. These families are evidently much nearer the stem form of the Lepidoptera than are those families in which media has been lost.

It does not follow that these families should be classed together. For each one may represent a distinct line of development. The presence or the absence of the base of media is a character that merely indicates the degree of divergence from a primitive type (see p. 43). The divergence in each case may be along a distinct line. It may be worth while to state in this connection that the families named above are nearly all of those of the Macrofrenatæ in which three anal veins are preserved in the hind wings, another character indicating a comparatively slight degree of divergence from the primitive type.

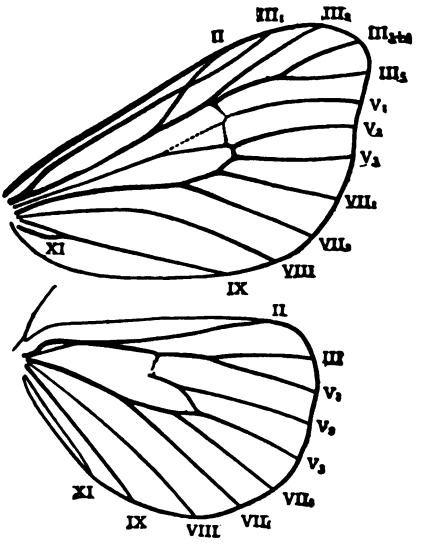

FIG. 17.—*Adoneta.*

Correlated with the abortion of the base of media is the coalescence of its branches with the adjacent veins. It follows from this that the extent to which this coalescence has gone is an indication of the degree of departure of a form from the primitive type. Compare, for example, the hind wings of *Packardia* (Fig. 16) with the hind wings of *Adoneta* (Fig. 17), two genera of the family Limacodidæ. In *Packar-*

dia, where a remnant of the base of media still persists, vein V_2 is merely connected with vein III by a cross vein. But in *Adoneta*, where the base of media of the hind wings is lost, vein V_2 has become consolidated with vein III for a considerable distance. It is obvious that in these respects, the loss of the base of media and the extent of the coalescence of veins III and V_2, *Adoneta* is the more highly specialized of the two genera.

It often happens that after the abortion of the base of media the discal cell is traversed by a more or less distinct line or scar indicating the former position of this part of the vein. This scar is indicated in the accompanying figure of the wings of *Eacles* (Fig 18) by dotted lines.

It will be observed that the branches of media are not continuous with the branches of this scar. There has been a migration of the proximal end of the remaining portion of each branch towards the vein from which it gets its supply of air. Frequently there remain short stumps, projecting into the discal cell from the discal cross vein, and continuous with the scar, at the points where the branches formerly emerged from the discal cell. These are indicated by the arrows in Figure 13, and are also shown in Figure 18. It will be readily seen that the extent to which this migration of the base of a branch has gone will serve as an indication of the degree of divergence of the form from a primitive type.*

In connection with this part of the discussion a few words regarding the nature of the so-called discal vein are appropriate. It is evident that this is not a single cross vein extending from radius to cubitus ; but it is made up of several distinct elements, and these elements may differ in different genera. There is a cross vein between radius and the first branch of media, and another between the third branch of media and cubitus (Figs. 16, 18, *c. v.*, *c. v.*). These extremes of the series forming the discal vein, however, have the appearance in many cases of being parts of longitudinal veins (Fig. 18) ;

* I wish here to acknowledge the assistance of Miss Clelia D. Mosher, who, while a student in my laboratory at Palo Alto, first worked out the relation of these stumps to the branches of media.

and in such cases have not been considered, heretofore, as parts of the discal vein. The intermediate portions of the discal vein may be merely the branches of media somewhat bent out of their primitive course. This condition is illus-

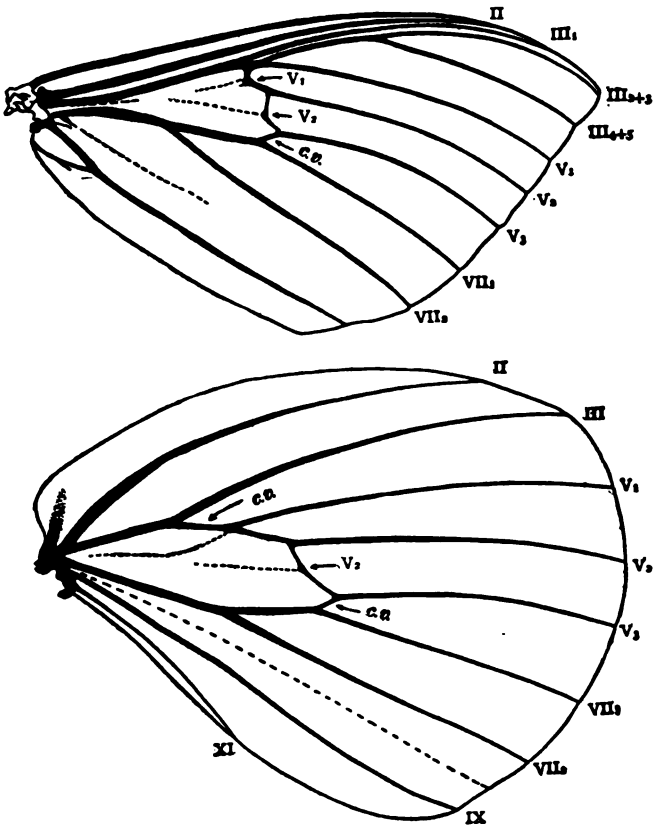

FIG. 18.—*Eacles.* The hind wing is enlarged more than the fore wing.

trated by the hind wings of *Packardia* (Fig. 16). Here the first branch of media has been drawn towards radius as a result of the change in the source of its air supply; and in a similar way the third branch of media, receiving a large part of its air from cubitus, is bent towards cubitus. In other

cases cross veins have been developed between the branches of media, and these form part of the discal vein; this is the case where there is an interpolated cell in the discal cell (Fig. 12). Sometimes a part of the discal vein may be looked upon as a trail indicating the path along which the base of a branch of media has migrated. An instance of this kind can be seen in the fore wings of *Eacles* (Fig. 18). Here that part of the discal vein lying between the stump which is marked V_1 and radius is the path over which the base of vein V_1 has migrated.

The union of vein V_1 with radius and of vein V_3 with cubitus after the abortion of the base of media is what would be expected. But in which direction would one expect the base of vein V_2 to migrate? Occupying an intermediate position between radius and cubitus it may go either way. It is like a stream in the middle of a level plain, a trifle may change its course. And thus we find that in some families it migrates towards cubitus, making this vein apparently four-branched, while in other families it goes towards radius, leaving cubitus apparently three-branched.

This difference may be looked upon as a difference in kind of specialization, and is frequently of high value as indicating a dichotomous division of the line of descent. It is obvious that in a family, where vein V_2 has migrated far towards cubitus and has thus established its chief source of air supply in that direction, it is not probable that genera will arise in which vein V_2 is more closely united to radius than to cubitus. To resume the figure, the plain through which the stream is flowing is an elevated plateau; a pebble may determine which of two slopes it shall descend; but when well started down one, it cannot traverse the other.

This character, however, must be used with care. In families where the direction of the migration of the base of vein V_2 has been firmly established, as in the Saturniidæ (Fig. 18), and in the Lasiocampidæ (Fig. 29), it is decisive. One need not hesitate a moment in determining to which of these two families a genus belongs. But there are other families in which the direction of this migration is not yet fixed; and here the character is of subordinate value.

Not only may the branches of one system of veins become joined to those of other systems as just described, but there are many forms in which two adjacent principal veins are coalesced to a greater or less extent. This occurs chiefly in the hind wings.

I will discuss the veins in regular order, beginning with costa. This vein is apparently wanting in the hind wings of most Lepidoptera, and but little can be said regarding the manner of its disappearance. It seems probable that in most cases it has simply become atrophied, the overlapping of the wings rendering it unnecessary or even undesirable. For when that stage in the development of the order was reached in which the two hind wings of each side overlapped to a considerable extent, was it not better that the costal margin of the hind wing should be flexible? There was no longer any need of a stiff margin, this part of the wing being supported during the downward stroke by the overlapping part of the fore wing; while a flexible margin would act as a valve to prevent the escape of the air between the two wings. The two wings in this way present a continuous surface. In many moths there is a thickening of the basal part of the costal margin; this I believe to be the remnant of costa.

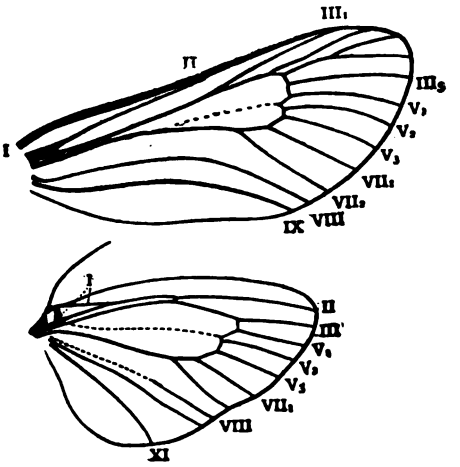

FIG. 19.—*Zygæna.*

But although it seems probable that in many cases the costa of the hind wings has simply faded out leaving cell I to function as this costal valve, there are cases in which this valve is a precostal development, the costa having moved

backwards and become consolidated with the subcosta. A good illustration of this is presented by the European genus *Zygæna* (Fig. 19). Here the costa and subcosta are distinct for a considerable distance, but become united into a single vein.

It will be observed that the basal portion of costa extends like a cross vein and forms a strong support for the frenulum. This part of costa is sometimes preserved when the remaining part is wanting. See figure of *Castnia* (Fig. 15).

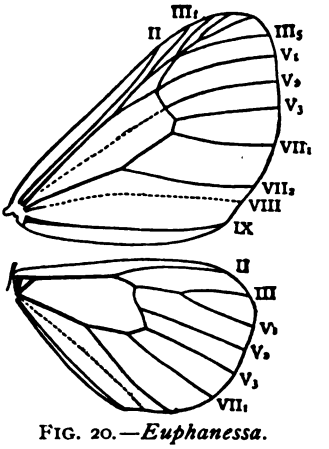

FIG. 20.—*Euphanessa.*

In most genera of the Geometridæ there is a faint indication of a remnant of costa extending from the humeral angle, at the base of the frenulum, to the subcosta, which is strongly angulated The same thing is shown in *Euphanessa*, (Figs. 20, 21), which is probably a Geometrid genus.

In many of the Psychidæ a remnant of costa is preserved (Figs. 22, 23). Here subcosta and radius are united for a considerable distance; then they separate and subcosta soon becomes joined to costa for a short distance. In Figure 23 I have represented what I believe to be the course of these three veins, slightly separating them where they are coalesced.

That part of subcosta that lies between its separation from radius and its union with costa appears like an oblique cross vein; and had the short spur that represents the terminal part of costa been lacking, its true nature would not have been suspected. Does not this arrangement of the veins in the Psychidæ afford an explanation of the origin of the so-called intercostal vein which is characteristic of the Sphingidæ? See Figure 24. In many butterflies the base

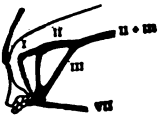

FIG. 21. — Humeral angle of hind wing of *Euphenessa.*

of costa of the hind wings is preserved. This is well shown in *Papilo* (Pl. II, 2). This vein has been observed and figured by many writers; but it has always been considered a precostal (*i. e.*, humeral) vein. But I believe it is essentially different from the humeral vein or veins of the Lasiocampidæ. The humeral veins of this family of moths are secondary developments; while the spur in the humeral angle of butterflies is a remnant of one of the primitive veins, the costa.

In the hind wings of many moths a coalescence of subcosta and radius also takes place to a greater or less extent. These two veins may be joined for a short distance, as in Packardia, (Fig. 16), or they may be merged into one for a considerable proportion of their length as in *Megalopyge*, (Fig. 25), and in the Sesiidæ. Every degree of coalescence between these extremes exist.

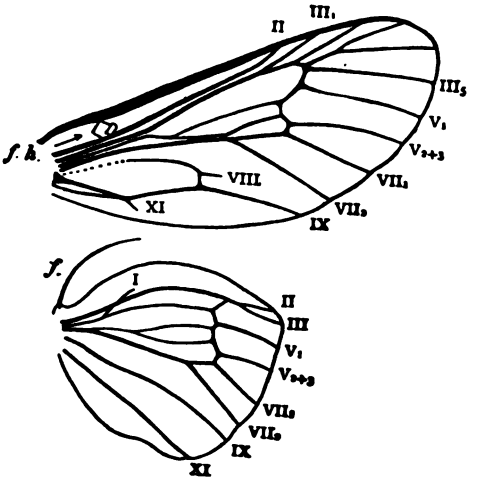

FIG. 22.—*Thyredopteryx.*

It has been customary in cases like the last to consider the subcostal vein wanting; but it is only necessary to count the branches of the principal veins to see that all are present; moreover, in most cases the two coalesced veins are separate for a short distance near the base.

FIG. 23.—Diagram of part of hind wing of *Thyredopteryx.*

There are, however, forms in which the basal part of radius is wanting. This condition is brought about in this way. First, something interferes with the growth of the basal part of radius, and this vein becomes weaker than the oth-

er principal veins. This stage is exhibited by *Prionoxystus*, (Fig. 12), in which radius of the hind wings still persists but is much weaker than the other veins, except media. Correlated with this weakening of radius is the formation of a cross vein between it and subcosta (Fig. 12, *c. v.*). This is an establishment of a new source of air supply for the distal portion of radius, and renders less necessary the basal portion of that vein. Sometimes the two veins are drawn together, and the

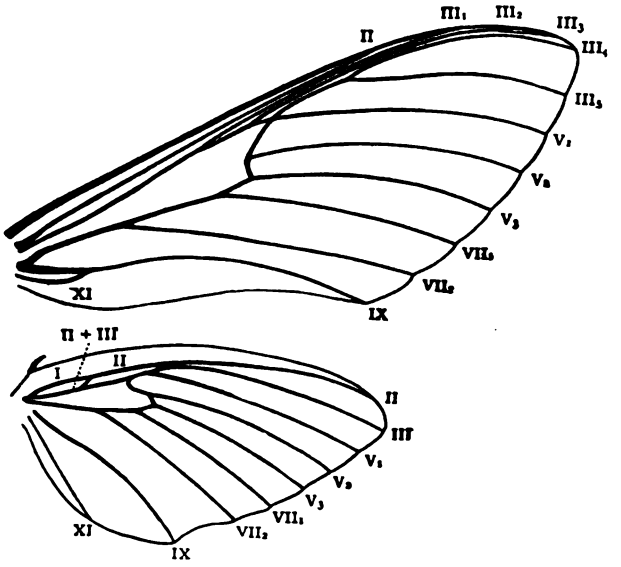

FIG. 24.—*Protoparce.*

coalescence extends in both directions from the point of first union, resulting in the form presented by *Megalopyge* (Fig. 25); but in other cases that portion of radius between the point of union and the base of the wing becomes atrophied. An approach to this condition is shown by *Acoloithis* (Fig. 26).

In the fore wings where radius is branched, we often find an anastomosing of the branches. In this way are formed the accessory cells (Fig. 20). This anastomosing doubtless serves to strengthen the wing.

In the hind wings of all Lepidoptera, except *Hepialis* (Fig. 27) and *Micropteryx* (Fig. 28), all of the branches of radius are united into one. But the condition of radius in the two genera named shows that it is normally five-branched in the hind wings as well as in the fore wings.

In the discussion of media, given on a previous page, attention was called, so far as concerns its coalescence with other veins, merely to its branches; but the principal stem of this vein may become joined either to radius, as in the fore wing of *Castnia* (Fig. 15), or to cubitus, as in the fore wing of *Prionoxystus* (Fig. 12).

It will be observed that here is a character which is of value as indicating a dichotomous division of the line of descent.

I do not recall any instance where cubitus is coalesced with an anal vein to a marked degree, except in the Papilionidæ (Pl. II, Fig. 2); but the growing together of different anal veins is a very common occurrence. This condition is preceded phylogenetically by the formation of a cross vein. Such a vein exists between veins IX and XI of the fore wings of *Castnia* (Fig. 15), and between veins VIII and IX of *Thyridopteryx* (Fig. 22). Following this stage the two veins are drawn together, See veins IX and XI of the fore wings of *Thyridopteryx* (Fig. 22), and the same veins in *Megalopyge* (Fig. 25). Usually, however, when these veins are joined in this way, that part of vein XI beyond the point of union disappears, and vein IX presents the appearance of being forked towards the base. See *Adoneta* (Fig. 17).

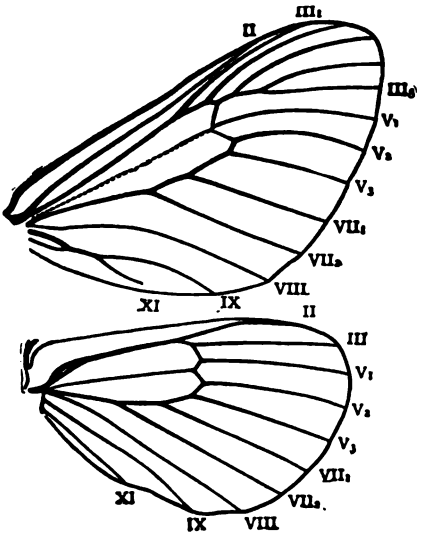

FIG. 25.—*Megalopyge.*

In the fore wings of the Psychidæ it frequently happens that the basal part of vein VIII disappears, and then vein IX appears to be forked outwardly (Fig. 22).

A good illustration of the coalescence of principal veins in another order of insects is presented by the dragon-flies (*Odonata*). Here veins III, IV and V are united into one from the base of the wing to the arculus. This coalescence is from the base of the wing outward, as is the coalescence of the main stem of media with either radius or cubitus in the Lepidoptera. But most instances of coalescence in the Lepidoptera begin on the disc of the wing and extend in either direction. In the Diptera a third mode of coalescence is common. In this order it frequently happens that two longitudinal veins come together at their tips and unite, the coalescence proceeding from the margin of the wing towards the base. The result is that a cell which normally opens on the margin of the wing is closed at a greater or less distance before the margin ; and the extent of this distance will be an indication of the degree of divergence from the primitive type.

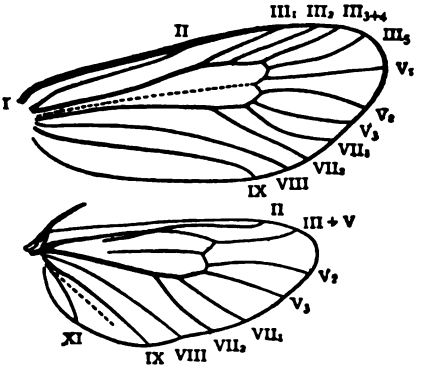

FIG. 26.—*Acoloithus.*

The coalescence of two veins may be complete resulting in the reduction of the number of veins in the wing. This frequently happens especially with the branches of radius of the fore wings in the Lepidoptera. This vein is naturally five-branched ; when a less number of branches occurs it is because the coalescence of some of the branches has proceeded to the margin of the wing.

The number of veins in the wing may be reduced, however, in another way : a vein may simply fade out. The most common instances of this kind in the Lepidoptera occur in the

anal areas of the wings. As these areas become narrowed (*i. e.*, specialized by reduction) one or two veins disappear.

The second branch of media is also a vein that is apt to disappear by atrophy; this occurs frequently in the Geometridæ.

The usual result of specialization of the wings of Lepidoptera is a reduction of the number of veins where any change in the number is made. But it is not always so; for new veins may appear. I have already described the formation of cross veins, where a new source of air supply is established, and preceding the coalescence of distinct veins. In a somewhat similar way veins are formed in the basal part of cell I of the hind wings in the Lasiocampidæ. In these cases the humeral angle has become greatly extended (Fig. 29). This outgrowth of the wing, like all other parts, is abundantly supplied with tracheæ; and about some of the tracheæ have been developed veins which protect them by stiffening this area so that it will not bend and thus compress them. This stiffening of the area doubtless serves another function to be described later.

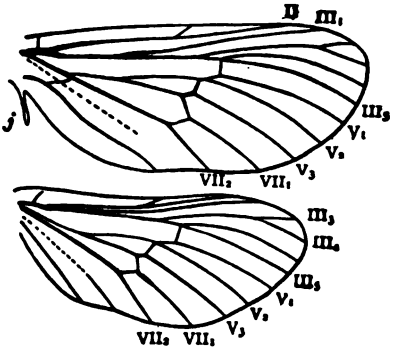

FIG. 27.—*Hepialis.*

These veins, developed in the humeral angle of the wing, I designate as the *humeral veins*. They have been termed the precostal veins; but the determination of the fact that the so-called costa of Lepidoptera is really the subcosta, renders the name precostal inappropriate.

The joining together of the two wings of each side in many moths by means of a frenulum and a frenulum hook, is a well known characteristic. But the real nature of the frenulum has not been understood, neither has its taxonomic value been appreciated.

I was led to make a careful study of this part of the wing by the discovery that in *Hepialis* an entirely different method of uniting the two wings of each side has been developed. In this genus, and as I have since discovered in *Micropteryx* also, instead of the wings being joined by a frenulum, which is a bristle or a bunch of bristles borne by the hind wing, they are joined by a membranous lobe extending back from near the base of the inner margin of the fore wing (Fig. 27, 28, j).

To this lobe I have applied the name *jugum*.

When the wings of *Hepialis* are extended, the jugum projects back beneath the costal border of the hind wing, which,

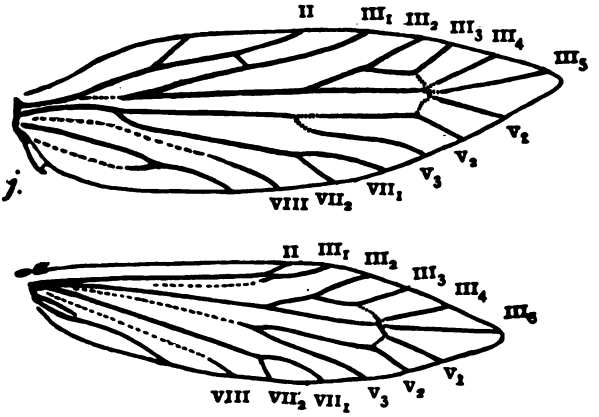

FIG. 28.—*Micropteryx*.

being overlapped by the more distal portion of the inner margin of the fore wing, is thus held between the two, as in a vice.

The discovery of the fact that there are two distinct modes of uniting the wings during flight suggests the inference that in the primitive Lepidoptera the wings were united in neither way. For it is not easy to see how one mode could have been developed from the other.

It is probable that in the primitive moths the mesothorax and metathorax were much more distinct than in the recent forms; and consequently the two pairs of wings were farther

apart than now. As the consolidation of the thoracic segments advanced, the wings were brought nearer and nearer together, till finally the development of a connecting organ was rendered possible.

Such an organ might be borne by the fore wings, or it might be borne by the hind wings. In some moths the specialization took the former direction; in others, the latter; and thus arose a division of the order.

This division I consider of subordinal value; and I have already proposed the names *Jugatæ* and *Frenatæ* for the suborders thus indicated.*

Let us try to obtain an idea of the ways in which the jugum and the frenulum were developed. As to the jugum I have but little to offer beyond the suggestion that at first it may have been merely an adventitious lobe, or a slight sinuosity in the inner margin of the fore wing. If such a lobe should project beneath the hind wing ever so little it would tend to insure the synchronous action of the two wings, and thus offer an opportunity for natural selection to act.

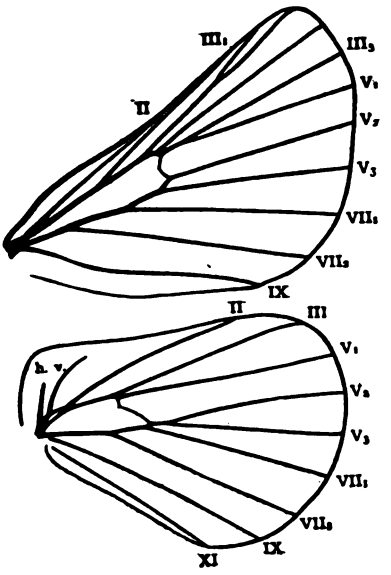

FIG. 29.—*Clisiocampa.*

The frenulum is a much more complicated organ. As a rule we find that in the female it consists of several bristles, while in the male it consists of a single, strong spine. If one of the bristles of the compound frenulum of the female be examined it will be found to be hollow, containing a single cavity. But when the frenulum of a male is examined it is found

* Proc. Am. Ass. Adv. Sci., Vol. XLI (1892), p. 200.

to contain several parallel cavities. Evidently the frenulum of the male is composed of several bristles as is that of the female, but these bristles are grown together, forming a single strong spine. This can be easily seen by examining a bleached wing that has been mounted in balsam. Usually the cavities in the bristles contain air which renders them easily visible.

It is obvious, therefore, that the frenulum of the female exhibits a more generalized condition than does that of the male. In some females the frenulum is so slightly developed that the bristles composing it are little more than hairs. This fact suggests that the primitive frenulum was developed from a bunch of hairs, clothing the base of the wing. Such a tuft of hairs projecting under the fore wing would tend in a slight degree to insure the synchronous action of the two wings; and as soon as these hairs had assumed this function the tendency of natural selection would be to strengthen them. In the female of *Prionoxystus* the frenulum consists of a series of bristles which vary in size from a short hair to a comparatively long spine (Fig. 12, *f*). This throws much light on the development of this organ.

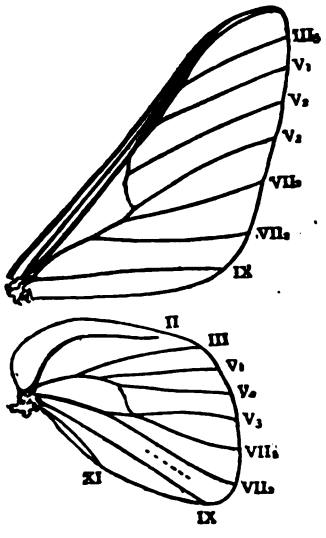

FIG. 30.—*Anisota.*

The extent to which the specialization of the frenulum has been carried is remarkable. In the males of some of the Psychidæ it is a strong spine nearly half as long as the hind wing (Fig. 22). In the Cymatophoridæ it is furnished with a knob at the tip. But the most remarkable feature of this specialization is the development of a membranous fold on the fore wings of males for receiving the end of the frenulum, and thus more securely fastening the two wings together.

This fold, or *frenulum hook*, is so well known that it is unnecessary to enter upon a detailed discussion of it. I will, therefore, merely record a few observations that I have made upon it. In all families in which I have observed it, it arises from the membrane of the wing near the base of cell I (Fig. 22), except that in *Castnia* it seems to have been pulled back so that it arises from the subcostal vein. The uniformity in the position of the frenulum hook indicates that it was developed before those families in which it exists had become separated phylogenetically. For if it had been independently developed in the different families there would probably have been a lack of uniformity in its position.

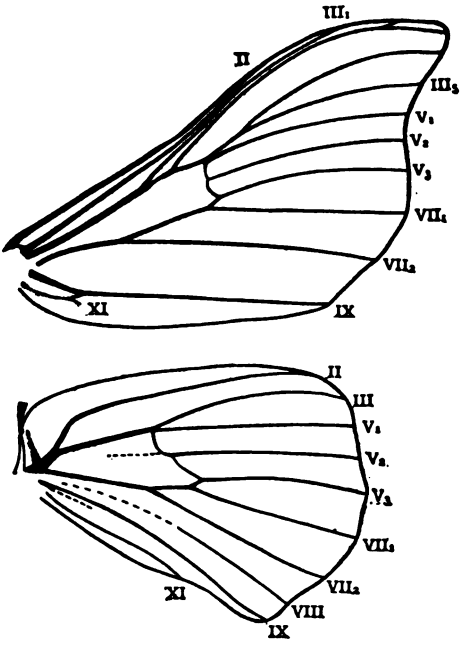

FIG. 31.—*Perophora.*

Some light is thrown upon the probable origin of the frenulum hook by the fact that in many females there is a tuft of curved scales projecting back from the base of cell I, and serving to hold the frenulum in place. In many moths there is also a tuft of scales projecting forward from the base of cell VII, which functions in a similar way.

In certain families of moths (Saturniina, Lasiocampidæ, and Drepanidæ) and in all butterflies there is neither a frenulum nor a jugum. But in other respects the wing characters of these moths and of butterflies agree quite closely with those

of the frenulum-bearing moths, and do not agree with the Jugatæ in their distinctive characters (*i. e.*, in an equal reduction of the two pairs of wings, and in having radius of the hind wings branched).

If the wings of one of these moths or of a butterfly be examined it will be seen that there is a large expansion of the

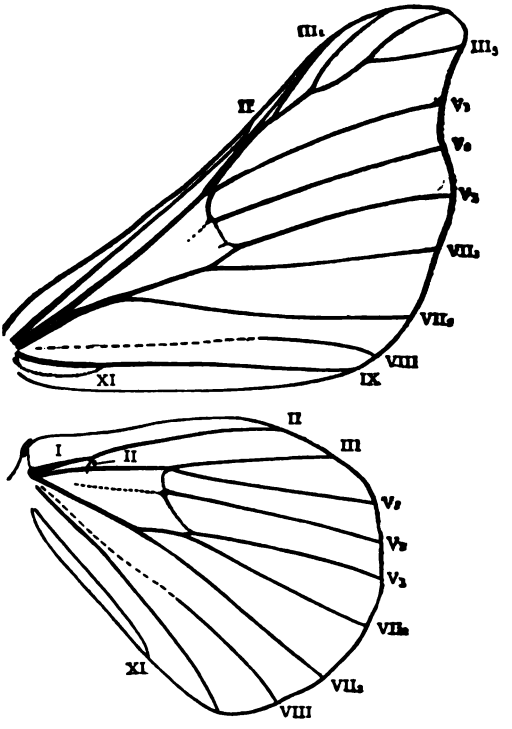

FIG. 32.—*Sericaria.*

humeral angle of the hind wings (Fig. 30, 14), which causes the two wings of each side to overlap to a much greater extent than they do in other Lepidoptera.

This extensive overlapping of the wings effectually insures their synchronous action without the aid of a frenulum, and I believe explains the loss of the frenulum. This theory is

supported by the fact that in the more generalized genera of the Saturniina (*Perophora* and *Sericaria*) where the humeral angle is not expanded to so great a degree as it is in the more specialized forms, there remains a rudiment of the frenulum, (Figs. 31, 32). And in the Drepanidæ where the frenulum is usually wanting, it persists in one sex in certain genera.

It is important that this expanded humeral angle should have a certain degree of stiffness if it is to perform the function of a frenulum. This has been obtained in some cases by a more or less diffused thickening of the membrane of the wing. Such a thickening is represented by the dotted portion in the figure of the hind wing of *Eacles*, (Fig. 18). In other cases the thickening takes place along a definite line and encloses a trachea; thus are formed the ***humeral veins*** of the Lasiocampidæ, (Fig. 29).

An interesting fact in connection with this abortion of the frenulum, is that in *Perophora* the rudiment of the frenulum of the male consists of a bunch of bristles. This is an excellent illustration of an organ which, in the course of its abortion, retraces the steps by which it was formed. In *Sericaria* the bristles composing the rudimentary frenulum in the male are still consolidated.

This modification of certain hairs on the costa of the hind wing into an organ whose function is to fasten the two wings together, is paralleled by the development of a row of hooks on the costa of the hind wings in the Hymenoptera and in the Aphididæ, which has a similar function. And the development of a jugum has taken place in the Trichoptera. In fact in several respects the Trichoptera and the Jugatæ resemble each other more closely than do the Jugatæ and the Frenatæ.

When a careful study is made of the wings of the two sexes of a species it often happens that a marked difference is found in them; and so far as I have observed the difference indicates a higher degree of specialization on the part of the male. It seems as if the female lagged behind the male in the race for perfection of organs. This is often shown in the degree to which the branches of the veins are consoli-

dated. But it is shown most markedly in the structure of the frenulum as already pointed out.

The explanation of this comparative lack of specialization of the wings in females is to be found largely, I believe, in the fact that the males seek their mates, while the females await the approach of the males. Many instances are well known (*Orgyia*, *Anisopteryx*, *et al.*) where the females have lost their wings through disuse while the males retain well developed wings. The only instance that I can call to mind where the reverse has occurred, is the case of *Blastophaga*. Here the male has no need of wings, as he finds his mate in the cavity of the fig in which he has been developed; while the female must fly elsewhere to deposit her eggs in a suitable place.

The great difference in the habits of flight of the two sexes in many moths is well illustrated by the results of a series of experiments with trap lanterns which I conducted several years ago. Six lanterns were kept burning from spring to fall, and each day's catch was kept separate. The results have been partially tabulated by Mr. Slingerland, and I extract the following table from his report.*

TABLE SHOWING THE NUMBER OF SPECIMENS OF EACH SEX OF TWO SPECIES OF FELTIA, CAPTURED WITH TRAP LANTERNS AT CORNELL UNIVERSITY IN 1889.

DATE.	*F. subgothica.*		*F. jaculifera.*	
	Males.	*Females.*	*Males.*	*Females.*
July 4	. . . . .	. . . . .	. . . . .	1
" 12	1	. . . . .	. . . . .	. . . . .
" 17	. . . . .	. . . . .	. . . . .	1
" 21	2	. . . . .	. . . . .	. . . . .
" 23	1	. . . . .	. . . . .	. . . . .
" 26	1	. . . . .	. . . . .	. . . . .
" 27	2	. . . . .	. . . . .	. . . . .
" 28	1	. . . . .	. . . . .	. . . . .
" 29	6	. . . . .	. . . . .	. . . . .
" 30	2	2	. . . . .	. . . . .
" 31	12	2	. . . . .	. . . . .
Aug. 1	7	2	. . . . .	. . . . .
" 2	19	. . . . .	. . . . .	2

* Canadian Entomologist, Vol. XXV, 81.

Date.	*F. subgothica.*		*F. jaculifera.*	
	Males.	*Females.*	*Males.*	*Females.*
Aug. 3	9	1	1	.
" 4	17	3	1	.
" 5	39	4	3	.
" 6	5	.	.	.
" 7	3	.	.	.
" 8	5	.	1	.
" 9	32	1	.	.
" 10	7	1	4	.
" 11	9	2	.	.
" 12	5	.	.	.
" 14	30	3	1	2
" 15	59	1	2	.
" 16	42	.	1	.
" 17	76	10	.	2
" 18	124	3	1	.
" 19	161	9	5	.
" 20	198	6	.	.
" 21	160	19	1	1
" 22	108	6	.	.
" 23	63	2	.	.
" 24	122	10	.	.
" 25	209	8	.	.
" 26	110	7	.	.
" 27	90	2	.	.
" 28	93	3	.	.
" 29	97	4	.	.
" 30	53	2	.	.
" 31	108	6	.	.
Sept. 1	60	8	.	.
" 2	65	2	1	.
" 3	50	.	.	.
" 4	87	4	.	.
" 5	23	.	.	.
" 6	37	2	.	.
" 7	8	.	.	.
" 8	16	3	.	.
" 9	1	.	.	.
" 11	1	2	.	.
" 14	1	.	.	.
" 16	2	1	.	.
" 17	1	.	.	.
" 18	.	1	.	.
Total	2240	142	22	9

Feltia jaculifera is not a very common species at Ithaca and hence the results obtained with this species are not so important as those obtained with *Feltia subgothica*. This is our most common Noctuid ; and of the specimens captured (2,382

in all) more than 94 per cent. were males. It is not at all likely that this represents the difference in the numbers of individuals of the two sexes; it is much more probable that the difference is due to a greater activity on the part of the males.

While I believe that the greater specialization of the wings of the male is due to the greater activity of that sex, I confess that I am greatly puzzled by the fact that in no female of the Macrofrenatæ has a consolidated frenulum and a frenulum hook been developed.* In other respects the females, as a rule, lag behind the males in their specialization only a short distance. But while the possession of a consolidated frenulum and a frenulum hook is attained by the males in the most generalized of living frenate moths, that stage is not reached by the females of the most specialized genera. Obviously there is a factor here that I have not discovered.

A similar lagging behind of the females is shown in a marked way in the specialization of the antennæ in the Saturniidæ. Here in the more generalized genera (*Coloradia* and *Hyperchiria*) the antennæ of the male alone are pectinate. In *Colosaturnia* the female has attained pectinate antennæ but unlike those of the male each segment bears only a single pair of pectinations. In the remaining genera of our fauna both sexes have pectinate antennæ and in each case each segment of the antennæ bears two pairs of pectinations; but the antennæ of the male are much more highly developed than are those of the female. If, as seems probable, the antennæ are organs of smell, and if, which also seems probable from certain well known experiments, the males in this family are guided to the females by the sense of smell, it is easy to understand the higher specialization of the antennæ of the males in this family.

In this discussion of the taxonomic value of the wings, I have confined myself chiefly to a study of the form of the wings, their venation, and the relation of the two pairs to each other. But I believe that even the clothing of the wings is of great taxonomic value.

*I have not studied the Microfrenatæ enough to be in a position to make generalizations regarding them.

If the scales of any of the more generalized moths be examined, they will be found to be long and narrow and scattered irregularly over the surface of the wing. On the other hand in the more specialized members of the order, as in most butterflies, the scales are much less hair-like, being short and broad; and they are arranged in regular overlapping rows. Evidently both the form of the scales and their arrangement upon the wing offer indications as to the degree of divergence from a primitive type of the insect bearing them.

More than this I am convinced that in some cases at least the form of the scales is characteristic of a particular line of development. One can determine, for example, without any doubt whether a moth belongs to the Lasiocampidæ or not by merely examining the scales of the wings.

I was impressed with the taxonomic value of the scales very soon after I began the systematic study of the Lepidoptera according to the method outlined in this essay. But the time at my disposal would not admit of my investigating this part of the problem in a satisfactory manner; and at my request the investigation has been undertaken by my colleague Professor V. L. Kellogg of the Leland Stanford Junior University.

Professor Kellogg is preparing an elaborate paper on this subject, which will be published soon after the appearance of the volume containing this one.

While the chief object which I have had before me is the indication of a method of taxonomic work, I hope this essay will be of value to entomologists in hastening the adoption of a uniform nomenclature of the parts of the wings of insects, and thus make easier the study of the relation of the different orders of insects to each other. In order that this nomenclature may be more complete I propose the following method of naming the cells of the wing; for we have as yet no system that is of general application.

The method I propose is, briefly, to designate each cell by the name or number of the vein that forms its front margin when the wings are spread.

The application of this system to the Lepidoptera is indicated by Figure 33.

In certain special cases special names may be desirable. Thus in the Lepidoptera the cells formed by the anastomosing of the branches of radius are commonly known as the *accessory cells*, which is a very convenient term. And cell III + V is universally known as the *discal cell*. In some of the more generalized moths a cell is formed within the discal cell by a forking of media: this has been termed the *interpolated cell* (Figs. 12, 22, 27).

In those orders where there are transverse veins, each of the cells between two longitudinal veins is divided into a series of

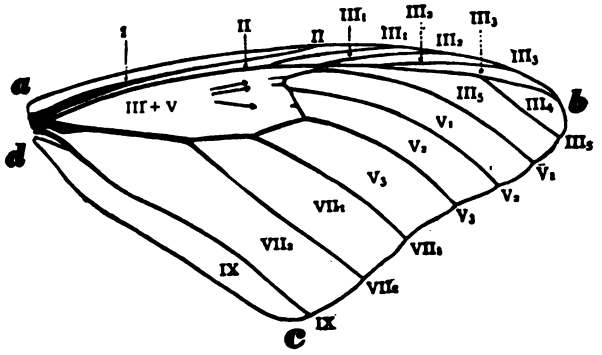

FIG. 33.—Fore wing of *Danais*, illustrating the nomenclature of the veins and cells. The numbers placed opposite the ends of the veins refer to the veins; the others, to the cells.

cells, and can be so designated. Thus the series of cells between veins III_1 and III_2 may be termed the first series of radial cells; and the members of such a series can be numbered. If one should speak of the peculiar form of the third cell in the second radial series, there need be no difficulty in determining the cell indicated, even by one who had not made a special study of the order to which the insect in question belongs. Heretofore it has been necessary for the student to learn a distinct nomenclature for each order, and in some cases for each family, studied.

In concluding this part of this essay I wish to refer to two curious methods of specialization that have interested me

greatly. In certain cases where the body of the insect has become greatly reduced in size, a reduction of the area of the wing membrane has taken place and correlated with this there has been a great expansion of the fringe of the wing. The best known examples of this are the narrow-winged Tineids, the Thysanoptera, and certain parasitic Hymenoptera. This kind of specialization seems possible only with minute insects, where the weight to be supported during flight is not great.

In a Tineid which I have studied the hairs composing the fringes of the wing are inserted in the lower side of the wing-membrane a short distance back from the edge of the wing; and the edge of the wing is stiffened above by strong overlapping scales. This arrangement renders the fringes rigid during the downward stroke of the wing, but admits of their depression during the upward stroke; a combination well adapted to facilitate flight.

The second method of specialization referred to above is the loss of the front wings in the Coleoptera and Euplexoptera. In these two orders the paraptera of the mesothorax have been developed into elytra, and have crowded out the front pair of wings. The function of flight has been relegated in this way to the hind wings.

This homology of the elytra of beetles with the tegulae of Hymenoptera and with the patagia of Lepidoptera was pointed out by F. Meinert long ago*; but Meinert's paper seems to have escaped the attention of entomologists almost entirely. It is referred to by C. Hoffbauer in his paper on the minute structure of the elytra.† But although Hoffbauer shows conclusively that the structure of the elytra resembles that of the pronotum and differs in every essential feature from that of the wings, strangely enough he does not accept the conclusion of Meinert.

Meinert also pointed out the fact that in many Coleoptera (*e. g.*, *Dytiscus*) rudiments of the front wings exist beneath the elytra.

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* Entomologisk Tidskrift, 1880, 168.

† Zeit. Wiss. Zool., LIV, (1892,) 579.

As to the cause of this strange specialization I can only conjecture that in the primitive Coleoptera the habits of the insects were such that the protection of the wings by elytra was of more importance than that the first pair should be functional; cephalization was sacrificed in order that the remaining pair of wings might be protected. It may be that the primitive Coleoptera were wood borers, the only paleozoic remains supposed to be of beetles are borings; or their habits may have been like those of the recent Carabidæ. In either case the wings would be in need of special protection.

PART III.

A CONTRIBUTION TO THE CLASSIFICATION OF THE LEPIDOPTERA.

In this place I purpose to state briefly the conclusions that I have reached regarding the phylogeny of the families of the Lepidoptera. These conclusions are the results of an effort to read the record of the action of natural selection as recorded in the wings of these insects. Owing to the limited time at my disposal, but little attention has been given to the evidence presented by other parts of the body; and for the same reason I have been able to study the Tineids, Tortricids, and Pyralids hardly at all. The following classification is, therefore, merely a provisional one; and is put forth chiefly as a record of the results that I have obtained up to this time in applying the method outlined in the preceding pages.

I confidently expect, however, that the principal conclusions stated here will be confirmed by a study of other parts of the body; for in Nature's court the testimony of different witnesses if rightly understood will agree. If any of the conclusions should prove to be incorrect, the fault will be found to lie with the translator and not in the record.

The fullness of the discussion that has already been given of the ways in which wings are modified will warrant considerable condensation in the following outline. I will first indicate the relations of the proposed divisions to each other by means of a table; and will afterwards give fuller characterization of these divisions.

TABLE OF PROPOSED DIVISIONS OF THE LEPIDOPTERA.

A. Suborder JUGATÆ.

B. *The Macrojugatæ* . . . . . Family HEPIALIDÆ.

BB. *The Microjugatæ* . . . . . Family MICROPTERYGIDÆ.

AA. Suborder FRENATÆ.

B. *The Microfrenatæ.*

C. *The Tineids* . . . . . Superfamily TINEINA.

CC. *The Tortricids* . . . . . Superfamily TORTRICINA.

CCC. *The Pyralids* . . . . . Superfamily PYRALIDINA.

BB. *The Macrofrenatæ.*

C. *The Frenulum-conservers.*

D. Moths in which the reduction of the anal area of the hind wings precedes the reduction of the anal area of the fore wings. This group is not represented in the North American fauna. *Castnia* (Fig. 15) will serve as an illustration.

DD. Moths in which the reduction of the anal area of the fore wings precedes the reduction of the anal area of the hind wings.

E. *The Generalized Frenulum-conservers.*

F. Moths in which a great reduction of the subcostal cell of the hind wings is taking place.

G. Moths in which the anal veins of the fore wings anastomose so as to appear to be branched outwardly. (Fig. 25.)

Family MEGALOPYGIDÆ.

GG. Moths in which the anal veins do not anastomose in such a way as to appear branched outwardly.

Superfamily ZYGÆNINA (in part).

FF. Moths in which the subcostal cell of the hind wings is not greatly reduced.

G. Moths in which the anal veins of the fore wings anastomose so as to appear to be branched outwardly. (Fig. 22.)

Family PSYCHIDÆ.

GG. Moths in which the anal veins do not anastomose in such a way as to appear branched outwardly.

H. Family COSSIDÆ.

HH. Family LIMACODIDÆ.

EE. *The Specialized Frenulum-conservers.*

F. DIOPTIDÆ.

FF. *The Geometro-Bombycids and the Geometrids.*

G. Family NOTODONTIDÆ

GG. Family BREPHIDÆ.

GGG. Family GEOMETRIDÆ.

FFF. *The Noctuo-Bombycids and the Noctuids.*

G. Family CYMATOPHORIDÆ.

GG. Family NOCTUIDÆ.

Family LIPARIDÆ.

Family AGARISTIDÆ.

Family ARCTIIDÆ.

FFFF. *Isolated Families of Specialized Frenulum-conservers.*

G. Family SESIIDÆ.

GG. Family THYRIDIDÆ.

GGG. Family SPHINGIDÆ.

GGGG. Superfamily ZYGÆNINA.

CC. *The Frenulum-losers.*

D. *The Frenulum-losing Moths.*

E. Moths in which cubitus is apparently three-branched. Superfamily SATURNIINA.

EE. Moths in which cubitus is apparently four-branched.

F Family DREPANIDÆ.

FF. Family LASIOCAMPIDÆ.

DD. *The Skippers.*—"Butterflies" in which all of the branches of radius of the fore wings arise from the discal cell. Family HESPERIDÆ.

DDD. *The Butterflies.*—Butterflies in which some of the branches of radius coalesce beyond the apex of the discal cell.

E. Butterflies in which cubitus of the fore wings is apparently four-branched. Family PAPILIONIDÆ.

EE. Butterflies in which cubitus is apparently three-branched.

F. Butterflies exhibiting no tendency to abortion of the fore legs. Family PIERIDÆ.

FF. Butterflies exhibiting a marked tendency to abortion of the fore legs.

G. Family LYCÆNIDÆ.

GG. Family NYMPHALIDÆ.

A. SUBORDER JUGATÆ

This suborder includes those moths in which the two wings of each side are united by a membranous lobe, the *jugum*, borne at the base of the inner margin of the fore wings (Fig. 27, j), and in which the anal area of the hind wings is reduced while the radial area is not. The most available recognition character is the similarity in venation of the two pairs of wings; radius being five-branched in the hind wings as well as in the fore wings.

B. THE MACROJUGATÆ.

Moths of medium or large size. The mouth-parts are aborted, and correlated with this there persists a comparatively generalized condition of the wings, which is shown by the absence of a jugum plate. The larvæ are wood-borers. This division is represented by a single family.

Family HEPIALIDÆ.

BB. THE MICROJUGATÆ.

Moths of minute size. Mouth mandibulate, with both mandibles and maxillæ fitted for mastication. This is doubtless the most generalized form of mouth-parts preserved in this order. Correlated with the presence of functional mouth-parts, these moths show a higher specialization of wing structure than exists in the Hepialidæ; there being a plate-like organ at the base of the costa of the hind wings, the *jugum plate*, and a series of spines; both of which act with the jugum in assuring the synchronous action of the two pairs of

wings. (Fig. 28). The larvæ are leaf miners. This division is represented by a single family.

Family MICROPTERYGIDÆ.

AA. SUBORDER FRENATÆ.

This suborder includes those moths and butterflies in which the two wings of each side are united by a frenulum, borne at the base of the costal margin of the hind wings, or by a substitute for a frenulum, a large humeral area of the hind wings (see p. 88); and in which radius of the hind wings is reduced to an unbranched condition, while in the more generalized forms the anal area is not reduced. The most available recognition character is the dissimilarity in venation of the two pairs of wings, due to the unbranched condition of radius of the hind wings, while this vein in the fore wings separates into several branches. (See Figs. 10–33, except Figs. 27, 28).

B. THE MICROFRENATÆ.

Moths of small, often minute, size. The mouth-parts are usually functional. The anal area of the hind wings is not reduced, having three anal veins except in certain minute forms where a broad fringe has been substituted for the membrane of this area.

This division of the order is the Microlepidoptera of authors less the Micropterygidæ. But the statement made in many books that the presence of three anal veins in the hind wings distinguishes this group from the Macrolepidoptera is incorrect, for many of the Macros. possess this characteristic.

I believe, however, that the retention of the maximum number of anal veins in the hind wings by the Microfrenatæ is an index of an essential character of the group; while in the Macrofrenatæ, when it occurs, it is merely an indication of a slight degree of divergence from a primitive type. In other words, I believe that in the Microfrenatæ the tendency of natural selection is to develop that mode of flight which requires broadly expanded hind wings. While in the Macrofrenatæ the tendency has been at first in all groups and con-

stantly in some to develop a mode of flight requiring narrow wings.

This division of the order includes three superfamilies. I have nothing to add to their well known characteristics.

Superfamily TINEINA.
Superfamily TORTRICINA.
Superfamily PYRALIDINA.

BB. THE MACROFRENATÆ.

Moths usually of medium or large size; a few are small. The anal area of the hind wings contains less than three anal veins except in some generalized families where the maximum number persists; but in these families this character is usually correlated with rudimentary or aborted mouth-parts (see p. 48); and merely indicates a slight degree of divergence from a primitive type.

To this division of the order belong the most generalized of living Frenatæ; but this division also includes the most specialized of all Lepidoptera. I therefore place it after the Microfrenatæ in an ascending series.

C. THE FRENULUM-CONSERVERS.

Under this head may be grouped those families of the Macrofrenatæ in which the two wings of each side are united by a frenulum. They are the families in which the tendency of natural selection is as a rule to conserve the frenulum, although in certain genera this organ may be greatly reduced.

The first separation of this group into divisions is indicated I believe by a difference in the order of reduction of the anal areas of the two pairs of wings. In one division (D), represented by *Castnia* (Fig. 15), the reduction of the anal area of the hind wings precedes the reduction of the anal area of the fore wings. In the other division (DD) the reverse is the case. As we have no representatives of the first division in the North American fauna, and as I have had but limited opportunity to study exotic forms, I will discuss only the second division, which includes those frenulum-conserving moths in which

the reduction of the anal area of the fore wings precedes the reduction of the anal area of the hind wings.

E. The Generalized Frenulum-conservers. — Moths in which the anal area of the hind wings retains three veins, and in which the base of media of one or of both pairs of wings is preserved. In all of these moths the second branch of media (vein V_2) tends to become united with cubitus, thus forming a four-branched cubitus.

This is to a certain extent an artificial division, being based on characters that represent merely a degree of divergence from a primitive type. But it is really much more nearly a natural division than would seem at first sight. For if we omit those Zygænids that are included in it, it consists of four families, each of which is comparatively little removed from the stem form of the Frenatæ, and each represents a complete line of development. It is a grouping together of several short stems that arise near the base of the genealogical tree. In the case of the Zygænids included here we have to do with generalized members of a line of development which has reached in its more specialized forms as great a degree of divergence from the primitive type as has been attained by any members of the order.

I place but little weight upon the divisions of this group of families indicated below and in the table above. It is merely a convenient distribution based on recognition characters, and is not intended to represent affinities. For I believe each of these families represents a distinct line of descent, between which and any other line we at present know no connection except that of the common progenitor of all Frenatæ.

F. Moths in which a great reduction of the subcostal cell of the hind wings is taking place, the subcosta and radius being grown together to near the end of the discal cell. (Figs. 10, 25.)

G. Moths in which the anal veins of the fore wings anastomose so as to appear to be branched outwardly, (Fig. 25) The extremely generalized condition of these moths is shown by the slight reduction of the anal areas, there being three anal veins in both fore and hind wings, although veins IX and XI of the fore wings coalesce to a considerable

extent. The clothing of the wings is also in an extremely generalized condition, (see p. 93), and the larvæ too represent a generalized condition, having ten pairs of feet, three thoracic and seven abdominal.

The coalescence of subcosta and radius of the hind wings reminds us of what occurs in several of the more specialized families. But these moths cannot be regarded as representing the stem form of any of those families, as this coalescence takes place here before there is any reduction of the anal areas, while in the more specialized families referred to the anal areas are reduced first. This group is represented by a single family.* There are two North American genera *Megalopyge* (*Lagoa*) and *Carama*. Family MEGALOPYGIDÆ.

GG. Moths in which the anal veins of the fore wings do not anastomose in such a way as to appear to be branched outwardly. Three American genera, *Acoloithus* (Fig. 26), *Triprocris* (Fig. 10), and *Pyromorpha*, fall under this head. They will be discussed later, when the superfamily *Zygænina* is reached.

FF. Moths in which the subcostal cell of the hind wings is not greatly reduced.

G. Moths in which the anal veins of the fore wings anastomose so as to appear to be branched outwardly (Fig. 22). These are the Bag-worm Moths. They too show a generalized condition of the wings in the presence of three anal veins in both fore and hind wings; although in certain forms it is difficult to make out all of the anal veins in the fore wings, as the base of vein VIII is often wanting. The females have lost their wings entirely. The peculiar type of venation of the wings of these insects can not be regarded as representing the precursor of any other known type. I therefore look upon these insects as representing a distinct line of development. The group is represented by a single family.

Family PSYCHIDÆ.

* This family has been monographed by C. Berge. See *Farrago Lepidopterogica. Contribuciones al estudio de la Fauna Argentina y paises limetropes.* An. Soc. Arg. XIII. See also *Zool. Jahresbericht, 1882.* This monograph seems to have been overlooked by American writers.

GG. Moths in which the anal veins do not anastomose in such a way as to appear to be branched outwardly. This group includes two families, which so far as their wing-structure is concerned are more closely allied to each other than is either of them to either of the preceding families. In each of the two families included here there is frequently exhibited a marked tendency towards the abortion of radius of the hind wings.

H. Moths in which the branches of radius of the fore wings tend to anastomose, forming an accessory cell or cells (Fig. 12). The larvæ are wood borers. Family COSSIDÆ.

HH. Moths in which the branches of radius of the fore wings do not anastomose (Fig. 16, 17). The larvæ are "slug-caterpillars" and feed on the leaves of plants.

Family LIMACODIDÆ.

EE. *The Specialized Frenulum-conservers.* — Moths in which the anal area of the hind wings is reduced, having less than three anal veins, and in which that part of media which traverses the discal cell is usually wanting.

This division of the order is a very extensive one, including the greater number of the moths; it is represented in our fauna by thirteen groups, which are either of family or superfamily rank.

In several cases a family seems to be quite isolated; while in other cases several families can be brought together into a single larger group. I recognize two such groups. But in neither case does the group seem to be sufficiently homogeneous to be regarded as a superfamily; it must be regarded in each case as a provisional arrangement, which will be of use until the affinities of the families are better understood. These two groups are defined under FF and FFF below. Under F and FFFF are grouped the isolated families.

F. The family Dioptidæ represented by the genus *Phryganidia*, which occurs in California, seems to represent a distinct line of development. For it presents a combination of characters that sharply distinguishes it from all other known members of our fauna. The anal area of the fore wing is reduced, vein IX alone being retained (Pl. III,

Fig. 6). In the hind wings veins IX and XI are well preserved and the distal part of vein VIII is represented by a slight thickening of the membrane. The second branch of media in both wings nearly retains its primitive position; in fact it can not be said that a tendency to migrate in either direction has been established, although the base of media is lost. In the fore wings the third branch of media, and in the hind wings both the first and third branches of this vein, have become consolidated in each case with the adjacent vein to a remarkable extent. Here is a high degree of specialization in one direction correlated with a comparatively generalized condition of certain other characters. Although subcosta and radius of the hind wings are closely parallel, they are distinct. The clothing of the wings is extremely generalized, consisting chiefly of narrow scales, with a single notch at the extremity, and scattered irregularly over the surface of the wing. The larvæ resemble those of some of the Notodontidæ. Family DIOPTIDÆ.

FF. *The Geometro-Bombycids and the Geometrids.*—Under this head I group three families that have been quite widely separated heretofore. This group includes those families of the Specialized Frenulum-conservers in which the base of the second branch of media (vein V_2) tends to migrate towards radius; or in other words, those Specialized Frenulum-conservers in which the tendency is to form a three branched cubitus. (See p. 76 for a discussion of the importance of this character.)

G. Moths resembling Noctuids in their general appearance, having heavy, strong wings; but readily distinguished from that family by the direction of the migration of the base of vein V_2. In this family there seems to be but little if any tendency to specialization of the humeral angle of the hind wings. (Compare with the Geometridæ below.)

Family NOTODONTIDÆ.

GG. Of this group I know only a single species, *Brephos infans*. I therefore hesitate to characterize it. I believe, however, that this represents its natural position.

Family BREPHIDÆ.

GGG. Moths in which the wings are usually delicate and very finely scaled. There seems to be a marked tendency in this family to a specialization of the humeral angle of the hind wings, and correlated with this a tendency towards the reduction of the frenulum, especially in the females of certain genera. This tendency, however, is a much later development than the corresponding tendency with the Frenulum-losers. A marked indication of the specialization of the humeral angle of the hind wings which is exhibited by most genera of this family is a bending forward into it of the basal part of the subcosta and an elongation of the frenulum brace.* Both of these features are well shown by *Euphenessa* (Figs. 20, 21), which doubtless belongs to this group, although it is commonly placed elsewhere. Family GEOMETRIDÆ.

FFF. *The Noctuo-Bombycids and the Noctuids.*—The members of this group can be recognized by a tendency of the base of vein V_2 to migrate towards cubitus, and thus form a four-branched cubitus, and an absence of the peculiar characteristics distinctive of any of the families grouped under the next division (FFFF).

G. Here belongs a small family, which, although apparently closely allied to the Noctuidæ, exhibits striking peculiarities of development. There is no tendency towards a uniting of the subcosta and radius of the hind wings (Pl. III, 4), a tendency shown in all other families of the Noctuo-Bombycid division. The migration of the base of vein V_2 is more marked in the hind wings than in the fore wings, where it nearly or quite preserves its primitive position. And the union of vein V_1 of the hind wings with radius is by means of a comparatively long cross vein, so that veins III and V_1 appear to separate before the apex of the discal cell. In the males the tip of the frenulum is knobbed. The genus *Leptina* commonly placed in this family belongs to the Noctuidæ.

Family CYMATOPHORIDÆ.

GG. The four families that follow I have not yet studied

* By the term *frenulum brace* I designate a sclerite situated on the costal margin of the wing between the base of the frenulum and the base of the wing.

sufficiently to warrant my expressing any views as to their relationships to each other. In the Arctiidæ we find the most marked tendency to the reduction of the subcostal cell of the hind wings, subcosta and radius being consolidated in some genera for the greater part of their length. (Pl. III, 1).

Family NOCTUIDÆ.
Family LIPARIDÆ.
Family AGARISTIDÆ.
Family ARCTIIDÆ.

FFFF. *Isolated families of specialized Frenulum-conservers.* —The families that are grouped together here agree with the Noctuids and the Noctuo Bombycids in the direction of the migration of vein V_2, the tendency being to form a four-branched cubitus. But each of the following families exhibit striking peculiarities of specialization which isolate it from all of the others as well as from the preceding group of families.

G. The clear-winged moths are placed here provisionally, although I believe that their true position is among the Microfrenatæ. But as I have studied them and the Microfrenatæ only superficially, I will not presume to make so radical a change. In this family there is a high specialization of the wings, although the anal area of the hind wings in many cases retains three anal veins. This is a combination of characters not found elsewhere in the Macrofrenatæ, but is quite characteristic of the Microfrenatæ.

Family SESIIDÆ.

GG. The Window-winged Moths exhibit a type of wing venation not seen elsewhere among moths. The most striking feature of it is expressed by saying that all of the branches of radius of the fore wings are preserved, and all arise from the discal cell (Plate III, Fig. 2). A similar type of venation is exhibited by the Hesperidæ (Plate III, Fig. 1). Whether this similarity has arisen independently, or whether it indicates a closer genetic relationship than has been assigned to these families heretofore I will not presume to say, with my present knowledge. The fact that in the Hesperidæ the frenulum brace is well preserved, may have some bearing on the settlement of the question. Family THYRIDIDÆ.

GGG. The Hawk-moths can be recognized by the well known form of their wings, and the presence of what has been termed an intercostal vein (Fig. 24). If I am correct in my interpretation of the homology of this vein, (see p. 78), the family can be characterized as those specialized Frenulum-conservers in which the base of costa of the hind wings is preserved and is remote from the costal border of the wing, and in which subcosta of the hind wings is consolidated with radius for a distance and then separates from radius and joins costa. This arrangement of the veins is quite different from that which exists in *Zygæna*, (Fig. 19), where also costa of the hind wings is preserved. It more closely resembles that of the silk worm, *Sericaria*! (Fig. 32.)

Family SPHINGIDÆ.

GGGG. I place the Zygænids last in this group of isolated families because it is among them that we find the most highly specialized representatives of the frenulum-conserving Lepidoptera, (*Cosmosoma*, *Syntomis*, Fig. 11). On the other hand certain genera, *Triprocris* (Fig. 10) and *Pyromorpha* present a remarkably generalized condition of wing structure. The range of variation is greater than I have observed in any other family or superfamily. In the more specialized forms a greater degree of cephalization of the powers of flight has taken place than occurs elsewhere in the order. And with this cephalization there seems to be correlated a lengthening of the fore wings and a narrowing of the basal part of the area lying between radius and cubitus of these wings. This narrowing of this area appears even in our most generalized forms, in which the discal cell of the fore wings can be well described as petiolate. Another characteristic of the Zygænina is the extent of the coalescence of the subcosta and radius of the hind wings. A somewhat similar coalescence occurs in certain genera of the Arctiidæ; but it takes place earlier (*i. e.*, in more generalized forms) in the Zygænina, and is carried farther than in the Arctiidæ. The Zygænids form a superfamily. The relationship of the families composing this superfamily have not been worked out. The American genera, so far as they are known to me, differ markedly from

Zygæna in the structure of the humeral area of the hind wings. In none of them is costa preserved. The American genera included here are *Acoloithus*, *Triprocris*, *Pyromorpha*, *Harrisina*, *Euchromia*, *Dahana*, *Didasys*, *Lycomorpha*, *Anatolmis*, and *Cosmosoma*. Of *Euchromia* I have studied only exotic forms; *Horama* and *Erruca* are unknown to me, but probably belong here also. The position of the Ctenuchidæ I have not determined. Superfamily ZYGÆNINA.

CC. THE FRENULUM-LOSERS.

This division of the order includes those families of Lepidoptera in which the frenulum has been supplanted by a greatly extended humeral area of the hind wings, (see p. 88). In some of the more generalized forms a rudimentary frenulum persists, (*Sericaria*, *Perophora*); in others it has been retained by the male (*Drepana*). This division includes three groups of families; the Frenulum-losing Moths, the Skippers (Hesperidæ), and the Butterflies.

D. *The Frenulum-losing Moths.*

E. Moths in which cubitus is apparently three-branched. Superfamily SATURNIINA.*

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*The following expresses my views regarding the affinities of the members of this superfamily:

A. Moths in which the base of costa of the hind wings is preserved remote from the costal border of the wing. This is shown by the presence of an "intercostal vein" (*Sericaria*, Fig. 32.) (See p. 78.) Frenulum preserved in a rudimentary state. Family BOMBYCIDÆ.

AA. Moths lacking an "intercostal vein." (These are the true Saturnians.)

B. Generalized Saturnians. In these vein V_2 retains its primitive position, midway between radius and cubitus; and there are three anal veins in the hind wings, the distal part of vein VIII being preserved (Fig. 31.) Frenulum preserved in a rudimentary state. Family PEROPHORIDÆ.

BB. More Specialized Saturnians. Vein V_2 of the *hind* wings apparently a branch of radius (Fig 30); anal area of hind wings with not more than two veins, vein VIII having been lost; frenulum entirely superseded by a greatly extended humeral area.

C. Antennæ of both sexes with only a single pair of pectinations to each segment. Family HEMILEUCIDÆ.

EE. Moths in which cubitus is apparently four-branched.

F. Humeral angle not strengthened by humeral veins. The frenulum is retained by the males in some genera. The North American forms represent three genera: *Drepana*, *Prionia*, and *Dryopteris*. Family DREPANIDÆ.

FF. Humeral angle strengthened by the development of one or more humeral veins. There are eight North American genera: *Quadrina*, *Gloveria*, *Thauma*, *Clisiocampa*, *Heteropacha*, *Artace*, *Tolype*, *Gastropacha*. Family LASIOCAMPIDÆ.

DD. *The Skippers.*—These are day-flying Lepidoptera, which resemble butterflies in usually holding their wings erect when at rest. They can be recognized by the peculiar venation of the fore wings, in which all of the branches of radius are preserved, and all arise from the discal cell. Although the frenulum is lost, the frenulum brace (see p. 106) is well preserved in some genera. See discussion of the Thyrididæ (p. 107) and compare the figures Plate II, Fig. 1, and Pl. III, Fig. 2. Family HESPERIDÆ.

CC. Antennæ of at least the males with two pairs of pectinations to each segment, excepting the terminal segments in some.

D. Antennæ of males pectinate for a little more than half their length. Family CERATOCAMPIDÆ.

DD. Antennæ of males pectinate throughout. Family SATURNIIDÆ.

BOMBYCIDÆ.—The superficial resemblance between this family and the next as shown by the single genus of each known to me (*Sericaria* and *Perophora*) is very striking. But a study of the structure of the wings shows marked differences (Figs. 31, 32). Note differences in the method of coalescence of the branches of radius of the fore wings, in the course of subcosta of the hind wings, and in the presence of an "intercostal vein."

Sericaria appears to represent a line of descent quite distinct from the true Saturnians as represented by the American forms. Do the "intercostal vein" of *Sericaria* and the caudal horn of its larva have any genetic connection with the similar structures in the Sphingidæ? This question suggests the desirability of a study of other Asiatic forms allied to *Sericaria*. It should be remembered that although *Sericaria* and the Sphingidæ belong to widely separated divisions of the order, *Sericaria* stands near the foot of one of them, being very generalized in structure.

PEROPHORIDÆ.—I propose the establishment of this family to receive the genus *Perophora*, the most generalized of the American Saturnians.

DDD. *The Butterflies.*—If we remove the Hesperidæ from this division of the order as indicated above, the butterflies form a well defined group. It contains, however, two distinct lines of descent which separated very early in the history of the group. In one, after the abortion of the base of media, vein V_2 migrated towards cubitus, forming a four-branched cubitus; in the other, this vein migrated in the opposite direction. There was also a difference in the order of the reduction of the anal areas of the two pairs of wings. See page 44 for a discussion of the importance of this character.

E. Butterflies in which cubitus is apparently four-branched; and in which the anal area of the hind wings is more reduced than the anal area of the fore wings. In the fore wings all three of the anal veins are at least partially preserved, while in the hind wings there is only a single anal vein. Pl. II, Fig. 2. Family PAPILIONIDÆ.

EE. Butterflies in which cubitus is apparently three-branched; and in which the anal area of the fore wings is

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I infer from the figure and description of *Lacosoma* that it also belongs here. *Perophora* has been classed in the Psychidæ merely because its larva is a case-bearer. But it presents no affinities to the Psychidæ, beyond belonging to the same suborder, even in larval habits. The case of the larva of *Perophora* is of an entirely different type from that characteristic of the Psychidæ.

HEMILEUCIDÆ.—This family represents a distinct line of development within the Saturniina, which separated from the branch giving rise to the Ceratocampidæ and Saturniidæ before the origin of the peculiar form of antennæ characteristic of these families. For although the Hemileucidæ lack this peculiar specialization, the extent of the migration of vein V_2 that has taken place in this family, indicates a higher degree of specialization in another direction than exists in any of the Ceratocampidæ or in the lower genera (*Coloradia* and *Hyperchiria*) of the Saturniidæ. This family is represented in this country by two genera, *Hemileuca* and *Pseudohazis*.

CERATOCAMPIDÆ.—I have nothing to add to the well known characteristics of this family. There are five North American genera: *Citheronia*, *Eacles*, *Sphingicampa*, *Anisota*, and *Dryocampa*.

SATURNIIDÆ.—We have eight genera representing this family; these are, beginning with the most generalized: *Coloradia*, *Hyperchiria*, *Calosaturnia*, *Telia*, *Actias*, *Saturnia*, *Attacus*, and *Samia*.

more reduced than the anal area of the hind wings, the former having a single anal vein, the latter two, Pl. II, Fig. 3. This group includes three families.

F. Butterflies exhibiting no tendency to abortion of the fore legs. Family PIERIDÆ.

FF. Butterflies exhibiting a marked tendency to abortion of the fore legs.

G. Family LYCÆNIDÆ.

GG. Family NYMPHALIDÆ.

The most important innovation in the classification of butterflies proposed above, after the removal of the skippers, is the dismemberment of the Family Papilionidæ of authors, and the raising of the Pierinæ to family rank. I propose this change unhesitatingly; for it seems to me that nowhere within the Frenatæ is a dichotomous division of a line of descent more clearly indicated than in this case.

If I am right in my conclusions the much mooted question as to which is the more highly specialized, the Papilionidæ or the Nymphalidæ, disappears. For we have to do, not with two elements of a single series, but with the tips of two distinct lines of descent, each of which represents the highest degree of specialization of its line.

It is difficult for one who has adopted the commonly accepted classification of the butterflies to realize the great extent of the gap that separates the Papilionidæ (as limited here) from the other families of butterflies. The branching off of the Papilionidæ took place long before butterflies assumed their present form. At the time when it occurred there had been no reduction of the anal areas, and vein V_2 had not begun its migration towards either radius or cubitus. This is as generalized a condition of wing structure as exists in any of the living Frenatæ.

The division between the Pieridæ on the one hand and the Lycænidæ and Nymphalidæ on the other is also well marked. If we compare the Pieridæ with the Lycænidæ, the more generalized of the last two families, we find that the Pieridæ exhibit a much greater specialization of wing structure (as shown by the extent of the consolidation of vein V_1 with

radius) than do the Lycænidæ; but the Pieridæ do not exhibit that specialization by reduction of the fore legs which is characteristic of the Lycænidæ and Nymphalidæ. In the Nymphalidæ we find not merely the extreme of the reduction of the fore legs, but an even greater specialization of the wings than exists in the Pieridæ.

ITHACA, N. Y.,
27 July 1893.

EXPLANATION OF PLATES.

PLATE I.

(*Engraved from nature by Anna Botsford Comstock.*)

Fig. 1.—*Smerinthus geminatus.*
Fig. 2.—*Hepialis argenteomaculatus.*
Fig. 3.—*Attacus promethea.*

In Figure 2 is represented one of the most generalized of living Lepidoptera; in Figure 1 is shown a form in which the wings are narrow, being fitted for rapid flight; and in Figure 3, one in which the wings are broad, being fitted for a different mode of flight.

PLATE II.

(*Drawn by E. P. Felt.**)

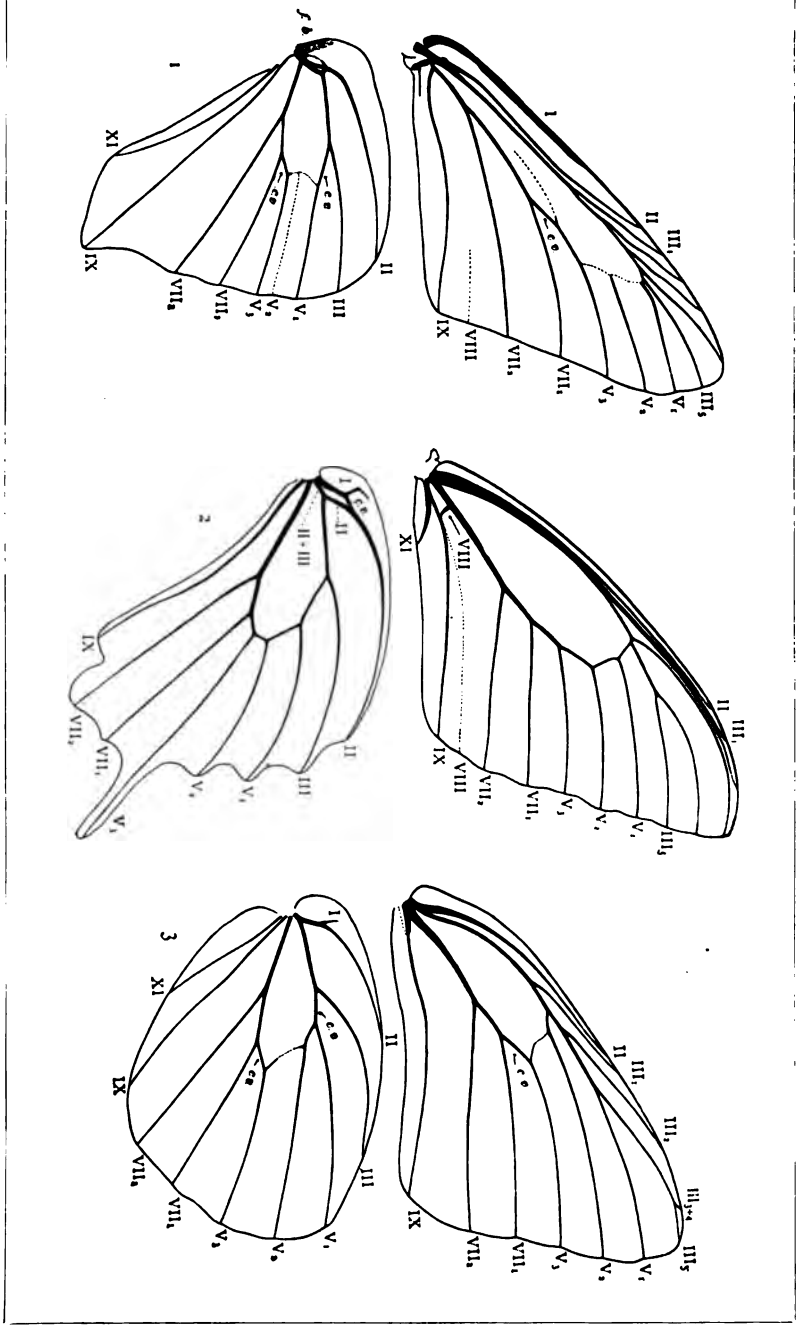
Fig. 1.—*Eudamus tityrus.*
Fig. 2.—*Papilio polyxenes.*
Fig. 3.—*Pieris protodice.*

PLATE III.

(*Drawn by E. P. Felt.*)

Fig. 1.—*Halisidota tessellata.*
Fig. 2.—*Thyris maculata.*
Fig. 3.—*Platephemera antiqua.*
Fig. 4.—*Thyatira scripta.*
Fig. 5.—*Hexagenia bilineata.*
Fig. 6.—*Phryganidia californica.*

*The figures in the text in the preceding pages were also drawn by Mr. Felt.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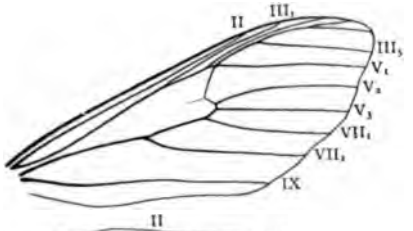
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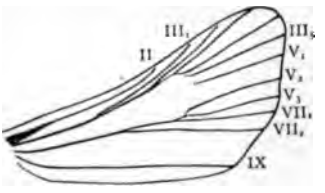
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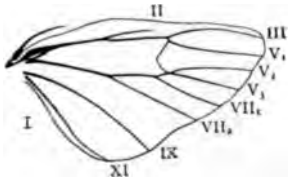
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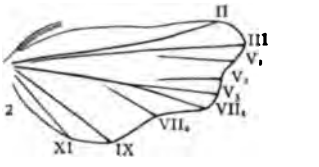
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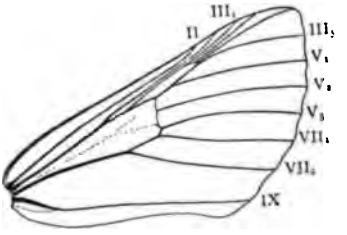
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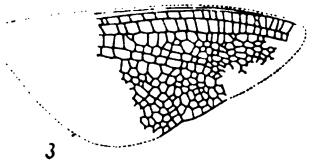
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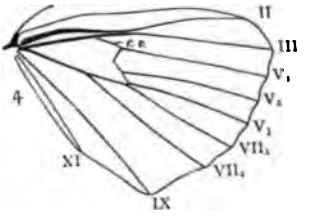
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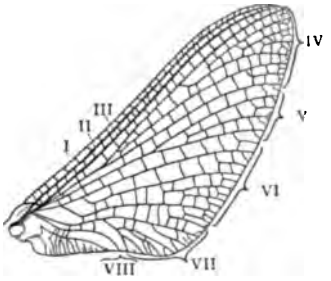
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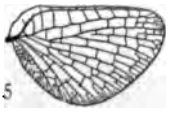
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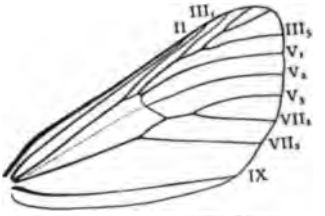
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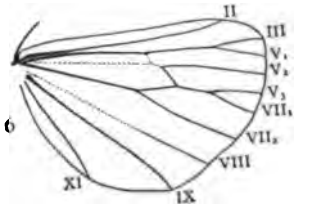
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THE VITAL EQUATION OF THE COLORED RACE AND ITS FUTURE IN THE UNITED STATES.

By EUGENE ROLLIN CORSON, B.S., M.D.

In June, 1887, I delivered a lecture before the Georgia Historical Society, entitled "The Future of the Colored Race in the United States from an Ethnic and Medical Standpoint." My object at the time was to refute certain writers who looked upon the colored race as a menace to our country, and whose sensational writings, prompted largely by political motives, were calculated to cause wrong impressions and unnecessary alarm. I attempted to show that a solution of the problem could be found outside the figures from the census, namely, in a study of the physical status of the race, their morbid tendencies, and their mortality compared with that of the whites.

As a practicing physician in a typical southern city, in a community where the colored almost equalled the whites, I felt I was in a position to study the subject. Only they who are brought into immediate contact with a race can form any adequate ideas of that race in all its bearings. They must see how they live and they must see how they die before they are qualified to judge of the race in its entirety, or atttempt to answer such a vital question as its future.

It is a significant fact that they who live in the South and who are brought into immediate relationship with the colored people are the last ones to look with fear on the future. They see but too plainly the many factors working against the race, inimical factors which come from within the race and not from outside. As the rise of a nation depends upon its own inherent powers, so its fall can be traced to causes within its ranks. Its enemies at home are more to be feared than its enemies abroad.

Since 1887, when I wrote my paper above mentioned, we have had another census. This last census, I am glad to say,

has fulfilled almost in every way the predictions then made, and I trust that with a fuller treatment of the higher mortality among the colored as compared with the whites, and the causes which have produced it, we can see with greater distinctness the future of the race.

In this present paper then I shall go over largely the ground treated in my first paper. I shall introduce the results of our last census, so far as the mere enumeration goes, —for the volumes on mortality and vital statistics are not yet out,—and finally elaborate certain pathological lines which were then but faintly drawn. This, I hope, in conjunction with the mortuary tables of our own city, will give us a fairly clear idea of the vital equation of the race, and by vital equation I mean that quantum and power of vitality which maintains individual life, for it is upon individuation, I believe, that racial strength and progress depend. And with high individuation goes a comparatively low death rate, especially in infancy and early childhood, and a high general average of age. Though the birth rate may be comparatively low, more infants born become mature and perfected individuals; there is more vitality for growth and development; racial traits and characteristics are stronger, with more power to hold the race together as a race. There is no better evidence of the great vitality of the Jewish race, for example, than their power to preserve their racial traits all over the world, and in spite of the many years of persecution and separation which they have had to endure.

After the tenth census of 1880, attempts were made to predict the future of the colored race from a few figures and the multiplication table. Gaps were filled in to suit each individual case and figures marshalled to suit the thesis. It was surprising how some allowed themselves to be run away with by these figures.

Professor E. W. Gilliam contributed an article to the *Popular Science Monthly* for Feb. 1883, entitled "The African in the United States" in which he drew for us a lurid picture of the future of our country. Here are his figures:

Whites in United States in 1880 (in round numbers),	42,000,000
Whites in United States in 1985 (in round numbers),	336,000,000
Northern Whites in 1880,	30,000,000
Northern Whites in 1985,	240,000,000
Southern Whites in 1880,	12,000,000
Southern Whites in 1985,	96,000,000
Blacks in Southern States in 1880,	6,000,000
Blacks in Southern States in 1980,	192,000,000

This is figuring with a vengeance. We may well tremble for the future of our country if these figures are even approximately correct. Their menace, Professor Gilliam thinks, is intensified by the second factor in his arguments, namely the impossibility of fusion of whites and blacks.

Mr. Albion W. Turgée attempted to reach the same conclusions in a book entitled "An Appeal to Cæsar." His book is a strange medley of figures, hypotheses, and circus-bill English. It is wholly unnecessary for us to quote from these writers or give any resumé of their arguments. It will not be amiss, however, to quote at some length from Mr. Henry Gannett's refutation which appeared in an article in the *Popular Science Monthly* for June 1885, entitled "Are we to become Africanized?" He gives here their arguments and refutes them by their own figures. In refutation of Professor Gilliam he writes :—

"An analysis of the author's curious method of deducing these results will, however, dispel this frightful vision of the future. The increase of white population between 1870 and 1880 was slightly less than ten millions. The number of immigrants during this period was a little in excess of two million eight hundred thousand. Subtracting the latter from the former, there is left a number which is 23 per cent. of the population in 1870, not 20 per cent., as Prof. Gilliam has it. But what does this 20 or 23 per cent. (it matters not which) represent? Certainly not the increase of native whites, as he interprets it. The census gives directly the numbers of native whites in 1870 and in 1880, and the proportional gain of this class during the decade was not less than 31 per cent. These are the figures he should have used in making his calculations.

"Now as to the increase of the colored element. Professor Gilliam at the outset, deducts from its rate of increase 5 per cent., representing about a quarter of a million persons, on account of the imperfections of the census of 1870. Concerning the omissions of this census little is known, except that they were generally distributed through the cotton States, were largely, if not mainly, of the colored element, and of that element, approximated nearer three-fourths of a million than one-fourth, and certainly exceeded half a million. Professor Gilliam's subsequent addition of 5 per cent. 'as an obvious consideration points to the conclusion that the blacks will for the future develop in the South under conditions more and more favorable,' certainly is not warranted by the facts or the probabilities, and, as we are reasoning from what has been and is, and not from what may be, it looks very much like begging the whole question.

"Correcting Professor Gilliam's statements, it appears that the ratios of gain during the past decade were, as nearly as can be known, as follows: For native whites, 31 per cent.; for blacks, not above 25 per cent.

"But all such comparisons, based upon the results of the ninth census, are utterly worthless. No reliable conclusions regarding the increase of negroes can be drawn from a comparison in which these statistics enter. The extent of the omissions can be a matter, within certain wide limits, of conjecture only. The only comparisons which yield results of any value are those made between the statistics of the eighth and tenth censuses. That the former was, to a certain slight extent, incomplete, is doubtless true, especially in regard to the colored element, but the omissions were trifling as compared with those of the ninth census. A comparison between the results of the eighth and tenth censuses shows the advantage to be clearly in favor of the native whites, who increased 61 per cent. in the twenty years, while the colored element increased but 48 per cent. This great increase of the native whites was effected in spite of the fact that the ranks of the adult males were depleted to the extent of over a million by the casualties of war, which the negroes scarcely felt."

In reply to Mr. Tourgée he writes:—

"In 'An Appeal to Cæsar,' by Judge Tourgée, the question of the future of the colored element is discussed from a somewhat different point of view. Without committing himself as to the increase or decrease of the colored element in the country at large, in proportion to the whites, the author finds, upon a somewhat superficial study of the statistics bearing upon the question, that in the South Atlantic and Gulf States the negroes have increased decidedly in proportion to the whites, while in those States which he classes as Border States they have relatively decreased. This massing of the negroes in what may, for convenience, be denominated the cotton States, coupled with the steady sharpening of the line of separation between the two races—a line which, as the author claims, becomes more and more accentuated as the inferior race increases in numbers and advances in education—will lead to inevitable conflict between the two races. As the negro becomes numerically the stronger, and, through education, appreciates more fully his present position, he will commence a struggle for the mastery, and then the days of the Ku Klux will be eclipsed in blood and slaughter. Such is the condition to which these ill-fated States are hurrying. To ward off this impending evil Judge Tourgée urges upon the general government the work of educating the blacks. Such, in brief is the 'Appeal to Cæsar.' * * * * * * * * * * * * * *

"It may, in passing, be suggested that a careful revision of his figures will show many important arithmetical errors, which may modify very sensibly some of his conclusions. It is unnecessary to follow his methods of reasoning, as the truth regarding the questions at issue can be arrived at much more directly. The fact is, that the negro is not migrating southward. There is no massing of the colored people in the cotton States. In 1860 the colored element of these States formed 66 per cent. of the colored element of the country. In 1880 it formed precisely the same proportion. Between 1860 and 1880 the colored element of the country increased 48 per cent. The same element of the cotton States increased, in this interval,

in precisely the same proportion, neither more nor less. These figures are conclusive upon this point, and from them there is no appeal.

"But the fact remains that, in these cotton States, the colored element was in 1880, in comparison with the white element, slightly stronger than it was twenty years before. This, however, is due not to a southward movement of the colored people, but to a decrease in the rate of increase of the whites of those States. While the increase of the native white population in the country at large between 1860 and 1880 was 61 per cent., that part of the same element resident in the cotton States increased but 39 per cent. This low rate of increase among the whites might seem to establish Judge Tourgée's position, though not in the way he states it, were it not for the fact that three-fourths of this increase took place during the decade between 1870 and 1880. The increase of whites in the South received a most effectual check during the four years of war, in which every male capable of bearing arms was in the field, and in which fully half a million laid down their lives. Since the war the white race has taken up a rate of increase equal to, if not greater than, that of the country at large, a greater rate than that of the colored people within its borders, and there is no apparent reason why they should not maintain it. It is not, then, a migration of the negroes southward which has caused their relative gain in these States, but it is the losses of the white race—losses which, however, are rapidly being repaired."

It will be interesting now to look to the deductions of the Eleventh Census, and see to what extent it agrees and where it differs from this succinct resumé of Mr. Gannett. I have before me Census Bulletin No. 48, giving the white and the colored population of the South for 1890. As that section of our country denominated the South Atlantic and South Central States with Missouri and Kansas, contained fifteen-sixteenths of the entire colored population of the United States, a race count of these states was made in advance of the main work of tabulation. The total population in this count was found to be 23,875,259, of which 16,868,205 were whites,

6,996,166 were colored, and 10,888 were Chinese, Japanese, and Indians.

The Bulletin goes on to state: "The abnormal increase of the colored population in what is known as the black belt during the decade ending in 1880 led to the popular belief that the negroes were increasing at a much greater rate than the white population. This error was a natural one, and arose from the difficulty of ascertaining how much of the increase shown by the Tenth Census was real and how much was due to the omissions of the Census of 1870. This question has been fully discussed in Bulletin No. 16, and it is now merely necessary to add that the tabulations herewith given sustain the theory already advanced, that the high rate of increase in the growth of the colored population as shown in 1880 was apparent, not real, and was due to imperfect enumeration in the Southern States in 1870.

"Attention is first called to Table I, on the following page, showing the white and the colored population of the states under discussion at each census since 1790, together with the number of colored to each one hundred thousand white and the percentage of increase respectively, of white and colored for the several decades.

"The table summarizes the entire case. In 1890 there were in the States under discussion 6,996,166 colored inhabitants, and in 1880, 6,142,360. The colored element increased during the decade at the rate of 13.90 per cent. The white population of these states in 1890 numbered 16,868,205, and in 1880, 13,530,408. They increased during the decade at the rate of 24.67 per cent. or nearly twice as rapidly as the colored element.

"In 1880 the proportion of white to persons of color in these states was in the relation of 100,000 to 45,397. In 1890 the proportion of the latter class had diminished, being then as 100,000 to 41,475.

Years.	Population.		No. of Colored to 100,000 White.	Per Ct. of Increase.	
	White.	Colored.		White.	Colored.
1790 . .	1,271,488	689,884	54,258	. . .	. . .
1800 . .	1,702,980	918,336	53,925	33.94	33.11
1810 . .	2,208,785	1,272,119	57,594	29.70	38.52
1820 . .	2,831,560	1,653,240	58,386	28.20	29.96
1830 . .	3,660,758	2,187,545	59,757	29.28	32.32
1840 . .	4,632,530	2,701,901	58,325	26.55	23.51
1850 . .	6,222,418	3,442,238	55,320	34.32	27.40
1860 . .	8,203,852	4,216,241	51,393	31.84	22.49
1870 . .	9,812,732	4,555,990	46,429	19.61	8.06
1880 . .	13,530,408	6,142,360	45,397	37.89	34.82
1890 . .	16,868,205	6,996,166	41,475	24.67	13.90

"During the past decade the colored race has not held its own against the white in a region where the climate and conditions are, of all those which the country affords, the best suited to its development.

"Referring again to this table, it is seen that in but three decades, that is, from 1800 to 1830, during a part of which time the slave trade was in progress, has the colored race increased more rapidly than the white. Since 1830 the white people have steadily increased at a more rapid rate than the colored. This increase has not been effected by the aid of immigration, for with the exception of Kansas and Missouri, these states have received comparatively few immigrants either from foreign countries or from the Northern States.

"Similarly the proportion of the colored inhabitants to the white increased somewhat between 1800 and 1830, but since that time it has steadily diminished. In 1830, when this proportion was at its maximum, there were nearly 6 colored inhabitants to 10 whites, but this proportion has been reduced to a trifle more than 4 at the present date, or by nearly one-third of its amount."

And again on page 5:

"The last two tables are of special interest as they illustrate the movements of the colored element during the past half century. An inspection of them makes it evident that there has been no extended northward movememt of this element since the time of the civil war. Indeed with the exception of

the District of Columbia, the border states appear to have lost rather than gained, and during the last decade there becomes perceptible a southward movement of the colored element from the border states into those bordering the Gulf, particularly into Mississippi and Arkansas, where they have increased proportionately to the whites. Let the states under consideration be divided into two groups, the first comprising Delaware, Maryland, District of Columbia, Virginia, West Virginia, North Carolina, Kentucky, Tennessee, Missouri, and Kansas, and the second, South Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana, Texas, and Arkansas. In the first of these groups the increase of the white population from 1880 to 1890 was at the rate of 22 per cent., while that of the colored element was but 5.50 per cent. In the second group the rate of increase of the white was 29.63 per cent., while that of the colored race was but 19.10 per cent. In the first group the number of colored to 100,000 white diminished from 80,116 to 73,608, or only 8.12 per cent. There is, therefore, a perceptible tendency southward of the colored people, which, while by no means powerful, has resulted in drawing a notable proportion of that element from the border states, and in producing in two of the far Southern states a more rapid increase of the colored element than of the white.

"Of the states under discussion, three, namely, South Carolina, Mississippi, and Louisiana, contained in 1890 a larger number of colored people than of white. Of the population of South Carolina more than three-fifths are colored. Five other states, namely, Alabama, Florida, Georgia, North Carolina, and Virginia, contained a colored element ranging from one-third to one-half of the population."

So much for the Census. This southward movement of the colored from the border states into the gulf states, is what we might naturally expect. The climate and soil are more congenial to the race, but more especially does it show an avoidance of contact and competition with the denser white population of the Northern, Middle, and Western States. The crowds of poor and alien whites which flock to us from Europe, throw themselves into the main streams of popula-

tion fearlessly, and we may say successfully, for with surprising rapidity they become an integral part of our white population. Though many fall by the wayside, many fight their way to the front. The struggle is not so great for them as in the older country. Of the same great race, brain and spine are equally pitted, and they run the same chances with the multitude. This southward migration then of the colored is a most significant fact.

Though I, of course, put a high value upon the census enumeration, I have always regarded the question of relative mortality as the pith of the whole matter. In the census enumeration there are many sources of error, and they have been most evident in several of the censuses. On the contrary, in a study of the relative mortality of the two races living together under similar conditions of soil and climate, the morbific tendencies which produce these racial differences come directly before the observing physician, and they soon become so evident that he who runs may read. I feel quite sure that there is not a competent physician practicing in the south among the two races who will not assure you promptly, that the colored race has not the vitality of the white race, and he will immediately show you in how many ways this has been brought home to him. A southern city, then, with a large population of white and colored, becomes a great "culture" ground where the many factors in the struggle for individual and racial life can be scientifically studied. I therefore purpose to show more plainly the sources of this greater mortality among the colored, and draw more sharply the perspective lines which lead to but one goal, the decadence of the negro as a race. To this end I have studied carefully the mortuary records of my own city, and I shall show that they tally fairly well with the mortality tables of the Tenth Census, prepared under the supervision of Dr. John S. Billings, in volumes XI and XII. The corresponding volumes to come of the Eleventh Census will show even more clearly, I believe, these great racial differences.

Reviewing the general mortality one is struck with the excessive mortality under the first year of life which in a meas-

ure is sustained up to the fifth year, when the vital forces having escaped Scylla at least, have gained sufficient headway to give the individual hope of passing Charybdis and of reaching the alloted term of life. Then reviewing the specified causes of death, we find consumption heads the list, followed by diseases of the nervous system, pneumonia, accidents and injuries, diarrhœal diseases, diseases of digestive system, malarial fever, measles, other diseases of respiratory system, diseases of circulatory system, diphtheria, affections of pregnancy, enteric fever, scrofula and tabes, venereal diseases, cancer and tumors, scarlet fever, diseases of urinary system, bronchitis, and diseases of the female generative organs.

The following table giving the age summary for the last nine years is of interest as showing the high mortality during the first year of life where the colored mortality more than doubles that of the whites. These figures must be viewed in a population of about 25,000 whites and 20,000 colored, or in that proportion. The mortality rapidly falls then for both races, reaching its lowest point between 5 and 10 years, the colored, however, more than doubling the whites. The mortality rises again for both races, reaching its highest point in the decade between 30 and 40, when it falls off again, and in the decade between 50 and 60 the mortality is about the same for both races. There is but little change in the decade between 60 and 70. Between 70 and 80 the colored mortality is greater again, becoming greater still between 80 and 90, and still greater between 90 and 100. This might lead one to think that the colored reach a greater age than the whites. But it must be remembered that the negro's age is usually much over estimated, that few know their right age and they are inclined to add any number of years, so proud do they feel of their senility. And, further, many of these negroes now rapidly passing away, are survivors of the old régime, when they were well cared for, and had reached at emancipation a safe age which kept them out of the struggle of life. They are relicts of better days for them, pure blooded negroes almost entirely, who passed their first fifty years in slavery, and under much better conditions for their physical well being than the new generation can boast of.

AGE SUMMARY TABLE.

Year.		1884	1885	1886	1887	1888	1889	1890	1891	1892	Average
Under one year . .	W	86	63	102	92	58	75	86	90	79	81+
	C	171	160	235	199	187	176	225	163	217	192+
Between 1 and 2	W	34	25	35	28	21	40	32	26	28	30−
	C	52	57	94	58	49	68	74	57	77	65+
Between 2 and 5	W	36	21	36	30	18	13	27	19	24	25−
	C	55	45	102	67	46	34	73	40	44	57+
Between 5 and 10	W	22	9	17	16	9	17	12	16	24	15++
	C	38	16	35	46	25	28	35	24	26	30++
Between 10 and 20	W	31	16	15	21	9	11	25	20	20	18+
	C	40	34	68	44	34	49	44	47	54	45−
Between 20 and 30	W	44	37	34	48	39	39	50	41	56	46
	C	87	84	101	93	91	92	101	103	99	94++
Between 30 and 40	W	58	49	47	49	43	48	61	52	54	51++
	C	77	75	88	86	68	60	81	83	103	80+
Between 40 and 50	W	45	24	43	49	51	35	54	54	51	45+
	C	51	59	64	55	45	65	60	70	69	60−
Between 50 and 60	W	37	32	56	54	41	29	52	52	39	43+
	C	37	35	44	54	33	35	47	45	47	42−
Between 60 and 70	W	43	25	41	45	44	48	50	47	46	43+
	C	32	42	44	44	29	29	46	55	39	40
Between 70 and 80	W	24	24	18	17	26	26	27	38	33	25+
	C	33	24	34	26	30	33	51	32	25	32
Between 80 and 90	W	5	7	7	9	11	3	9	6	13	7+
	C	18	22	20	19	19	8	23	23	22	19++
Between 90 and 100	W	1	1	2	2	1	0	2	3	0	1++
	C	12	6	7	5	3	4	10	4	10	6+
Over 100	W	0	0	0	0	0	0	0	0	1	½
	C	0	0	0	0	3	4	1	0	2	1+
Total	W	466	333	452	460	366	384	479	464	468	430+
	C	703	659	936	796	665	685	870	746	834	772+

These figures are not large enough, neither do they extend over a sufficient number of years, to draw entirely conclusive generalizations from, still they are suggestive, and show at least the high infant mortality which has such an important bearing on our subject. It is the mortality of the early years of life

which decides virtually the general mortality, and on the contrary, the reduction of this infant mortality points to a higher vital equation. I give here a table showing the relation of the mortality up to the fifth year to the total mortality for the colored for the last nine years.

YEAR.	*1884*	*1885*	*1886*	*1887*	*1888*	*1889*	*1890*	*1891*	*1892*	Total.
Total mortality, . .	703	659	936	796	665	685	870	746	834	6894
Mortality up to 5th year, ...	278	262	431	324	282	278	372	260	338	2825

These figures show that about 41 deaths out of 100 occur before the fifth year.* Here is a similar table showing the white mortality :

YEAR.	*1884*	*1885*	*1886*	*1887*	*1888*	*1889*	*1890*	*1891*	*1892*	Total.
Total mortality, . .	466	333	452	460	366	384	479	464	468	3872
Mortality up to 5th year, ...	156	109	173	150	97	128	145	135	131	1218

* To quote to any extent from the Tenth Census in the relation of age to deaths would swell this paper beyond its proper limits. If the reader can refer to Section IV, p. xxiv, Vol. XI of this Census, he will find some interesting tables, not only comparing the cities with the rural districts, our own states with the countries of Europe, but also the two races in those parts of our country where the colored exist in any number. The two tables on p. xxxii give the proportion of deaths for each age or groups of ages for white and colored, and show the much greater mortality of the colored under one year, and under the fifth year.

"In the southern groups, among the colored population, over half the deaths of males reported, or 507.16 per 1000, under 5 years of age, and for colored females, 438.47 deaths out of every 1000 reported are under 5 years." The greatest mortality among infants under one month occurs in Charleston, where the deaths for white males are 571.4, and for the white females 647.7 of each 1000 deaths under one year.

This shows for the whites during the last nine years that a little over 31 deaths out of 100 occur before the 5th year of life, almost 10 per cent. less than the colored. Of course it must constantly be borne in mind that these figures are for the city, and that the mortality in the country is much less for both races. But it is only from the cities that we get any accurate returns, and more important still, that this is the very point at issue, namely, the mortality of the two races when brought into direct contact and sharp competition. And it is this large source of error in the returns from the country which vitiates the general returns given in the census, and especially so in the returns of deaths among the country colored. Like a bird's-eye view, it shows a large area but no distinct outlines or details.

We have had recently some interesting figures from Japan bearing upon this question. It seems that Japan is a paradise for children; they are well cared for, and the greatest attention is given to their food. In 1872 the population was 33,110,000 and in 1890 it had risen to 40,070,000. Mr. Ourakami attributes this great increase to the low death rate among infants. "It appears that next to France Japan has the lowest birth-rate of any known country, but this is counterbalanced by the conservation of infant life. In fact, in point of infant mortality, Japan at present stands next to England among the nations of the world. Thus while in Russia the death-rate per 1,000 among children under 5 years of age is 423, in Bavaria 405, in Austria 390, in France 341, in Prussia 335, in Japan it is 276, and in England 255."*

Without having any proper birth-returns to show the mortality per 1,000 among colored infants, the figures in the above tables, if joined to the large number of still-births and premature births, show an exceptionally high mortality, higher than any figures given above. On this point I have no doubt. This is without question the pivotal point in the matter, and I shall go into some details to bring into relief its main features. I shall indicate the causes of ante-natal

*The Medical Record, March 18, 1893. p. 352.

mortality, of the death of the child at birth and during the lying-in-period, and finally of the dangers besetting it during its first years of life.

Despite the prolificness of the negress, the child *in utero* has many chances against its coming to term. The temptations and irregularities of illegitimacy swell the list of premature and still-births, and the number reported is but a poor showing of the real number of cases. They are looked to by "grannies" and ignorant midwives. The fœtus before the viable age is gotten rid of and finds no record at the Health Office, while the viable child usually dies from neglect and carelessness, if not from criminal measures. The mother practically receives no treatment, and she is soon up and about, with her uterus and adnexa in a diseased state.

Although I have no figures to bear me out, I am persuaded that the prolificness is lowered, and that the liability to miscarriage is increased, by miscegenation. This has certainly been my experience, and is in accord with the generally lowered vitality resulting therefrom.

It is of course well known that the poisons of syphilis and gonorrhœa both favor a throwing off of the product of conception. In the colored this is seen with redoubled force, due to the fact that both these diseases are apt to be virulent with them, and also that they do not realise their dangers or take the trouble to be properly treated. Again the very early age at which they become infected adds to the dangers from this source. The high types of fever, vaguely styled bilious, gastric, malarial remittent, and conjestive, to which the colored are by their occupation more exposed, and to which they have become more and more susceptible, frequently result in miscarriages. I have seen it follow tuberculosis pulmonum, general tuberculosis, pneumonia, and measles, to all of which diseases the colored are liable, and which prove very fatal to them. The usual causes which operate with the whites operate with them, and, as all the returns show, with even greater effect. The following table I have made up from the mortuary reports of the last nine years :

Year.		1884	1885	1886	1887	1888	1889	1890	1891	1892	Total.
Still-births, . .	W	25	29	19	24	33	25	34	42	21	252
	C	78	133	144	101	97	122	116	116	133	1040
Premature do	W	14	10	7	20	19	20	21	24	32	167
	C	14	11	5	16	33	34	25	19	20	177

It will be seen here that the still-births are more than three times as numerous among the colored as among the whites, but that there is virtually no difference in the returns of premature births. It must be remembered that with premature births they can more easily evade the law, and that they will avoid reporting their cases whenever they can. It is only necessity which compels many to get a burial permit. Naturally, therefore, these figures must be far from the truth.

According to the Tenth Census, vol. XII, p. LXXV, "The proportion of deaths reported as due to infanticide is highest among the colored population, being 14 out of each 100,000 deaths from specified causes, while for the whites in the same regions it is 5, and in the large cities 3, and in the rural districts 5 per 100,000." The poor returns from the rural districts account for the last figure which, of course, is incorrect. And again: "It will be seen from table 75 that the proportion of infants reported as still-born is much greater in the cities than in the country, decidedly greater among those of German than among those of Irish parentage, and somewhat greater among the colored race than among the whites. A certain number of cases reported as still-born are really cases of infanticide."

From the nature of the case the returns must be especially imperfect; the mortality from child-birth naturally calls for mention here. By far the largest portion of the colored employ midwives, only calling in a physician when there is dystocia, and even then they wait till the eleventh hour, endangering the life of both mother and child. These midwives are usually dirty, ignorant, and meddlesome, often changing a natural presentation into an unnatural one, im-

perilling both mother and child. It is not uncommon to find a midwife vigorously rubbing the abdomen of the poor puerpera, in view of helping the pains, and producing a more or less complete version of the child. The woman is delivered in a small room, all air and light shut out, and the atmosphere reeking with the emanations of the anility of the neighborhood, who have come in to view an event which has always the charm of a novelty. To these cases the physician is frequently called to meet all possible forms of dystocia, dangerous to both mother and child. Puerperal convulsions are more common among them than among the whites, and the mortuary tables show twice the mortality among the colored. I have myself attended twenty-two cases of this disease, 8 whites and 14 colored, with two deaths among the whites and six deaths among the colored. Of the children, four died among the white and nine among the colored. In many cases I was only called in after much precious time had been lost.* My case book will show all possible presentations and complications. I may mention placenta prævia, ruptured uterus, large uterine fibroids to which the negress is especially liable, puerperal septicaemia and peritonitis, neglected retained placenta and all its dangers. And I may mention lacerations of the cervix and perineum, and vesico-vaginal fistula. I mention these because there is a common belief among those who do not know, that the negress is like her African sister, who, living in a savage state, is free from these complications of the modern civilized woman. She is not only liable to them, but from neglect and improper treatment suffers more than the white. This must affect her prolificness with even greater force in the future. In going over the reports in the last nine years, I find the figures too meagre and the diagnoses often vague, so that it has but little value to us, except as showing that the mortality among the colored exceeds that of the whites, about in the proportion of 2 to 3.

* See my paper in the *Medical Record* for Oct. 24, 1891.

Year.		1884	1885	1886	1887	1888	1889	1890	1891	1892	Total.
Child birth	W	0	0	2	0	0	0	0	1	2	5
	C	1	1	5	3	2	0	5	1	3	21
Puerperal convulsions	W	4	1	2	1	3	0	0	1	0	12
	C	0	1	3	2	3	4	3	0	2	17
Puerperal fever	W	1	1	0	0	2	2	1	2	2	11
	C	4	3	0	0	2	0	6	0	2	17
Puerperal metritis	W	0	0	0	0	0	1	0	0	0	0
	C	2	0	1	1	0	0	2	2	0	3
Puerperal peritonitis	W	0	1	0	3	0	0	2	1	1	7
	C	0	0	0	0	0	0	2	0	0	7
Puerperal phlebitis	W	0	1	0	0	0	0	0	0	0	1
	C	0	0	0	0	0	0	0	0	0	0
Puerpera	W	0	0	0	0	0	0	0	0	0	0
	C	0	1	0	0	0	0	0	0	0	1
Puerperal thrombus	W	0	0	1	0	0	0	0	0	0	1
	C	0	0	0	0	0	0	0	1	0	1
Placenta prævia	W	0	0	0	1	0	0	0	0	0	1
	C	0	0	0	0	0	0	0	0	0	0
Metrorrhagia	W	0	0	0	0	1	0	0	0	0	1
	C	0	0	0	0	0	0	0	1	0	1
Puerperal septicaemia	W	0	0	0	0	1	2	0	0	0	4
	C	0	0	0	0	0	0	0	0	0	0
Miscarriage	W	0	0	0	0	0	0	1	0	0	1
	C	0	0	0	0	0	1	0	1	1	3
Abortion	W	0	0	0	0	0	0	1	0	0	1
	C	0	0	0	0	0	0	0	0	1	1

Referring to the Tenth Census I find the following statement in regard to deaths from child-birth: "The following table shows by grand groups the proportion of deaths from child-birth and from abortion per 1000 deaths from known causes, with distinction of rural and cities, and for certain

grand groups, for white and colored, and of Irish and German parentage. It will be seen from this table that the mortality in child-birth is about twice as great in relation to the deaths from known causes in the colored female as it is in the white, and that it is markedly greater in those of German than it is in those of Irish parentage. The same rule holds good as regards abortion although the difference is less marked. A large proportion of deaths due to criminal abortion are reported as deaths from peritonitis, which is the cause in part of the excess of deaths in females reported as due to that disease.*"

The colored infant comes into the world under very adverse circumstances, and the many dangers besetting it before its fifth year make one wonder it ever reaches maturity.

One of its first dangers is trismus nascentium. The following

Year.		1884	1885	1886	1887	1888	1889	1890	1891	1892	Total.
Trismus Nascentium	W	11	4	4	3	5	1	3	3	2	36
	C	28	40	39	34	27	14	17	11	22	232

figures make the colored mortality from this disease more than six times that of the white. Modern research has shown the cause of tetanus to be a bacillus common in garden mould. Here is a case of marked racial susceptibility. The filthy way in which the infant is dressed renders it still more liable. I have never seen a case recover; and here in our city alone 232 colored infants have died from this disease in the last nine years!

I give here for comparison the cases of tetanus in the adult for white and colored for the last nine years.

Year.		1884	1885	1886	1887	1888	1889	1890	1891	1892	Total.
Tetanus . . .	W	0	2	2	1	4	2	0	4	2	17
	C	3	4	4	4	2	3	1	2	3	26

* Vol. XII, p. lxxi.

Though the colored mortality exceeds that of the whites, the disparity is much less than in the case of trismus nascentium.

According to the Tenth Census the proportion of deaths from tetanus and trismus nascentium are for the whites 33.5 and for the colored 39.3 per 1000 deaths from known causes. I cannot think that these figures are reliable. The much greater susceptibility of the negro is generally recognized.

Gastro-intestinal diseases, with their accompanying disordered digestion and malnutrition, carry off the largest proportion of white infants and young children. With all nations it is among the poor and overcrowded that we see the highest mortality, where ignorance and poverty swell so greatly the death list. These factors, of course, exist among the colored to a large extent, though I do not think they ever have to endure anything like the lethal influences of the tenement life of our great cities. Living in warmer climates they escape the sufferings of intense cold poorly provided for, and their homes which consist of one-story frame houses or huts, are infinitely better, with all the dirt, than the small rooms and high stories of the city tenements. If the colored had to live under such conditions the infant mortality would greatly exceed that of the tenement poor of the great cities as well as their own present death rate. Fresh air and proper, clean food, would probably reduce this death rate one half. This important factor of proper food never enters the head of the ordinary colored mother. Even when liberally provided with nature's food, the breast is soon discarded for dirty feeding bottles and all sorts of abominations. You will frequently see a colored child, the canines not yet through the gums, sitting up at the table taking its regular dinner with the older members of the family, a dinner consisting of rice, greens, bacon and pot-liquor, and perhaps other abominations besides. This child may stand this better than the white child, but for all that it pays dearly for its smartness.

As a result of this we find gastro-intestinal catarrhs in all their forms, with reflex congestions of brain and other organs. The data from the mortuary tables are unsatisfactory so far as

knowing the exact state of affairs, because the diagnoses sent in are from different standpoints, and symptoms put down instead of diseases or pathological states. For example, many cases are put down as "convulsions" or "teething" which give us no record of the real pathological condition present. Again, many appear as *cholera infantum*, which covers a multitude of sins. My own experience has been that real *cholera infantum* is rare among us, comparatively speaking.

To try and clear up somewhat this unsatisfactory nomenclature, I have picked out of the mortuary tables the diseases common during infancy and childhood and have arranged them in three main groups.

I have in this table only put down those diagnoses which are recognized as children's diseases, and which are of sufficient importance to be considered as factors in the death-rate. Where there is doubt of the case being infant or adult, or, for example, under enteritis, which, morever, only includes a few cases, I have omitted them. This table will give us a fair idea of the relative mortality of the two races. They can be divided into three groups. "Congestion of the brain," "convulsions," "meningitis," and probably the most of "dentition," and "worms," are but different expressions for closely allied pathological states of the brain and nerve centres. Again, "cholera infantum," "entero-colitis," "thrash," "inanition," "intestinal catarrh," and "marasmus," are all related to the gastro-intestinal tract. And there is a third group comprised under diphtheria, whooping-cough, membranous croup, measles, and scarlatina, diseases recognized as having a specific germ origin.

Year.		1884	1885	1886	1887	1888	1889	1890	1891	1892	Total.
Congestion of the brain	W	20	8	10	19	13	14	14	16	17	131
	C	16	9	15	21	11	10	20	8	11	121
Convulsions	W	12	12	11	17	6	13	5	12	6	94
	C	52	39	40	32	34	24	38	36	31	326
Dentition	W	3	3	3	0	3	4	0	1	1	18
	C	20	17	23	9	20	17	20	15	17	158
Meningitis	W	8	6	13	6	5	4	4	13	16	75
	C	14	3	9	2	3	4	4	5	6	50
Worms	W	0	0	1	0	0	0	0	0	0	1
	C	4	2	4	0	0	2	4	0	0	16
Cholera infantum	W	19	11	0	19	8	13	17	12	12	111
	C	18	16	0	18	17	16	20	14	14	133
Entero-colitis	W	6	3	5	1	1	21	9	9	11	66
	C	4	1	11	1	3	10	21	12	15	78
Thrash	W	0	0	0	3	1	1	0	5	3	13
	C	0	0	0	11	0	4	0	0	1	40
Inanition	W	8	4	12	37	0	17	0	0	0	115
	C	17	14	30	3	0	0	0	0	0	4
Intestinal catarrh	W	0	0	1	11	0	0	0	0	0	17
	C	0	0	6	16	19	15	24	20	12	156
Marasmus	W	13	12	25	31	34	18	43	33	17	249
	C	30	14	29	4	5	4	0	12	18	83
Diphtheria	W	23	14	3	3	1	2	0	0	1	15
	C	4	1	3	0	3	0	13	6	2	27
Hooping cough	W	0	1	2	0	6	0	16	6	3	51
	C	0	7	13	0	2	0	0	0	3	14
Croup membranous	W	4	0	3	2	2	0	0	1	3	19
	C	1	1	1	1	1	1	4	2	0	20
Measles	W			8	3	2	1	1	0	0	40
	C			28	5	1	5	1	0	13	16
Scarlatina	W	0	2	1	0	0	0	0	0	3	7
	C	0	0	4	0	0	0	0	0		

Examining this table a little more closely, we find under "convulsions," a great disparity between the two races, at least three to one in favor of the whites. But when we turn to "meningitis" and "congestion of the brain," we find

larger figures for the whites in both cases. This shows, I think, that "convulsions," "meningitis," and "cerebral congestion," represent nearly the same thing, and taken together we have 497 deaths among the colored against 300 among the whites. So under "worms," death probably came through reflex cerebral trouble, or wasn't "worms" at all. The diagnosis, of course, has no weight and we can merely conjecture the cause of death. Put together we get a mortality about double that of the whites, the figures standing 844 for the whites against 1405 for the colored.

In the second group we find a great disparity between the races under "inanition" and "marasmus," while under "cholera infantum" and "entero-colitis" the figures almost correspond. Here, too, careless diagnoses have been made, and with no proper understanding as to nomenclature. As I have already said, cholera infantum is not a common disease here, but is mistaken for intestinal catarrh and entero-colitis, two diseases which are common here and which carry off great numbers of colored children. Putting this group together, we find a mortality among the colored fully double that among the whites.

Diseases of the nervous system stand second, and diseases of the digestive system fifth and sixth in the order of frequency as causes of death in the general mortality, and we can see their influence here in the infant mortality. It is, however, especially in this latter group that the colored so far exceed the whites. To the practicing physician it is the first great factor which is brought home to him in a comparison of the vitality of the two races.

In the third group we have diphtheria, membranous croup, scarlatina, measles, and whooping-cough. Diphtheria and membranous croup are now generally regarded as one and the same disease, and both are more common in whites than in colored, one of the few instances where the colored can boast of less susceptibility. And scarlatina which is so often accompanied with diphtheria, is also less common among the colored. But measles and whooping-cough are both very much more fatal among them. Of measles the Census gives

the proportion of 9.1 among the whites to 17.7 among the colored per 1,000 deaths from known causes, and our table tallies well with these figures. Cases of whooping-cough become broncho-pneumonia with brain complication and convulsions.

As the mortuary tables do not give the proportion of infants and young children, I have had to limit myself in the above table to recognized infantile diseases, but from my own experience I can state positively that bronchitis, broncho-pneumonia, and pneumonia are common among the colored children and very fatal. Broncho pneumonia is the form most commonly met with, and many cases put down as pneumonia are, strictly speaking, this form of the disease.

The great heat of the summer, especially the *vitiated* heat in the large cities, is a most potent factor in raising the death rate among the infant population. This factor holds with much less force in the southern cities from the fact that houses are built more open, of one or two stories only,—I speak of the homes of the poorer classes,—and the summers, while much longer than the northern summers, have not that intense heat, and most important still, the air is not so vitiated as it is in districts where high brick walls prevent a proper ventilation. Yet I see many cases of high fever among colored infants and young children, with symptoms of cerebral congestion and inflammation, and with a high mortality, due to a direct exposure to the sun's rays. This is a danger which is absolutely unheeded by the colored masses. It is a frequent cause of death. The whites are more careful in this respect and suffer less. What is known as sunstroke, *ictus solis*, due to a hot *vitiated* air, is not so common in the south as in the close cities of the north and west.

As I shall show later, tuberculosis in the form of pulmonary phthisis, carries off almost twice as many colored as whites. This affects chiefly the adult population. With our increasing knowledge of tuberculosis, we find its path of destruction becoming broader and broader. At the time of Koch's discovery of the tubercle *bacillus*, its field of operation seemed to be limited to the lungs. It was soon found, however, that

scrofulous glands, hip-joint disease, Pott's disease, and chronic bone and joint affections, were also caused by the same germ.

The bacillus attacks the human body at all points, and while the respiratory tract seems to bear the brunt of attack, it is found that the percentage of infection here is by no means so greatly superior to that of other organs or mucous channels. In 1,000 autopsies, cited by Osler, there were 275 cases with tubercular lesions, or over one-fourth. In the surgical clinic at Wurzburg, among 8,873 patients, 1,287, or about one-seventh were tuberculous, the bones and joints being involved in 1,037 cases. The post-mortem statistics of Harris and others show that over one-third —perhaps over one-half—of the people who live to middle age have some form of tuberculous infection. *

With these figures, and knowing how even with white children the large majority of cases of meningitis are tubucular, and how frequent it is in gastro-enteric lesions, how much greater effect must the bacillus have in the more susceptible colored child. Careful autopsies in the many cases of meningitis, gastro-intestinal catarrhs, in "marasmus," "inanition," "convulsions," and "dentition," would undoubtedly reveal this malignant germ. We may almost define the term "vital equation" to be the sum total of those forces which resist the bacillus tuberculosis.

From what I have here given, hardly more than in outline, the great influence of this high rate of infant mortality must be very apparent. And it cannot be explained solely by the fact that the colored population represents almost entirely the poor and ignorant class, with all the evil influences of poverty ignorance, dissipation, and general unhealthy living,—for it must be remembered that there is a fair contingent of whites in equal poverty, hunger and dirt,—but that the negro is more susceptible, has less powers of endurance, and succumbs more readily to the same diseases. Verily, the mills of God grind fast! Even the high prolificness of the race *under favorable conditions* could not keep pace with this mortality. On the contrary, a lower birth rate as naturally follows a lesser vitality

* The Medical Record, March 18, '93, p. 337.

as a higher death rate. Man has no such compensatory prolificness to meet a higher death rate as exists perhaps in some lower forms of life.

Consumption heads the list of the causes of death. Its importance becomes apparent when it is recognized that about one-sixth of all deaths are due to this disease. Of its greater fatality among the negroes there can be no question, and in our southern cities where the two elements come together in large numbers, the mortality among the colored about doubles that of the whites.

The following table shows the mortality in our city from 1884 to 1892 inclusive:

YEAR.	*1884*	*1885*	*1886*	*1887*	*1888*	*1889*	*1890*	*1891*	*1892*	Total.
Tuberculosis pulm. W	53	52	49	56	59	42	75	63	45	494
Tuberculosis pulm. C	98	102	107	109	103	99	125	128	114	985

I have not thought it necessary to estimate the deaths per 1000 of population, for the exact population is an uncertain element, and all figures must be only an approximation at the best. It will be amply sufficient for our purpose if these figures are viewed in a population where the whites are somewhat in excess.

A careful examination of the various board of health reports of our different southern cities and states will all show a remarkable uniformity on this point. To give anything like a full report on this subject from our different cities would swell this paper far beyond its proper limits, and I shall merely state that having examined the reports from Charleston, Richmond, New Orleans, Memphis, Nashville, Chattanooga, Knoxville, Columbus, Atlanta, and Mobile, I find that they tally well with our own tables.

The Tenth Census states:

"The total number of deaths reported as due to consumption during the census year was 91,270, being the greatest

number reported as due to any single cause of death." (Vol. XII, p. lviii.)

And further:

"It will be seen that the great majority of the deaths from consumption occur between the ages of 15 and 65, the greatest proportion in any decennium occurring between the ages of 20 and 30. The proportion of deaths between the ages of 15 and 35 is greater in the female than in the male. If we take the group of ages from 15 to 65 and compare the number of deaths reported as due to consumption with the total number of deaths from specified causes at the same group of ages, we find that the proportion is greatest in large cities, being, per 1,000,000 deaths, for males, 307,154, and for females, 338,571, while in the rural districts it is, for males, 218,455, and for females, 298,583. At the same group of ages in those regions where distinction of color and percentage are made, the proportions are, for whites, in each 1,000,000 deaths, males, 242,842, females, 302,046; for colored, males, 248,179, females, 326,973; for those of Irish parentage, males, 309,507, females, 375,636, and for those of German parentage, males, 249,498, females, 254,958. From these figures it would seem that the proportion of deaths from this cause in the colored race is but slightly greater than in the whites, and that it is greatest of all in the Irish. At ages under 15 a great excess of deaths from this cause is reported in the colored race." (Vol. XII, p. lix.)

These figures, I am sure, are very unreliable. The census admits the imperfect returns from the colored, and a review of Table III, p. xxi, Vol. XI, will show that the only returns from registration cities, which give a comparative mortality for the two races, are Louisville, Washington, Richmond, Baltimore, New Orleans, and Charleston, very inadequate returns to attempt anything like an accurate, comprehensive survey.

Turn to the diagram on p. xxxvii, showing for whites, colored, and Indians, the proportion of deaths from specified diseases in 1,000 deaths from known causes, and it will be found that the Indian mortality from consumption is almost

one-third greater that the colored, which, with our present light on the subject, must be a great error. It simply shows that the Indian returns have been more complete. And the same applies to the excessive mortality among the Irish. The cities drawn from have had this element of their population especially large. All this but convinces me the more that we can draw more accurate conclusions from a small section with complete returns than a superficial survey of a large territory with incomplete returns.

To the physician treating the disease among the colored, its great fatality is but too apparent. I can hardly recall a case where I have stayed it, and they die without the slightest response to treatment, and in a very short time. I have on many occasions been able to trace its contagiousness, several members of the same family going down in succession, the same room and the same bed serving for all. No one can doubt its contagiousness from such experiences. Soon after Koch brought out his lymph, I tried it very prudently with a mulatto but with such terrible aggravation that I never dared attempt it again.

So far as my experience goes, I have failed to find among the colored, many cases of local tubercular trouble, outside the lungs, brain, or elementary tract, and I explain it by this very great susceptibility. Local tubercular processes of skin, bone, or mucous membrane, of any duration, presuppose a certain amount of resistive power on the part of the body, preventing its becoming pulmonary or general. It is kept local. I do not believe the negro can long have a tuberculous focus in any part of the body without its rapidly becoming pulmonary or general. Further, my experience teaches me that the mulatto is more susceptible than the pure negro. It is with them that I have mostly seen those galloping cases which defy all efforts to restrain.

I have never seen a case of lupus in the negro, of tuberculous lesions of the bones I have seen but few cases. I can recall but few cases of tubercular peritonitis upon the diagnosis of which I felt any confidence. Tuberculosis of the genito-urinary organs I believe is more common, as following in the wake of gonorrhœal infections.

I have been assured by physicians who practiced among them before the war, and when their physical condition was so much better than it now is, that consumption was almost unknown. The finding of any tubucular lesion in the lungs at an autopsy was always a surprise. I shall, however, speak of this later.

I have mentioned in my first paper the great susceptibility of monkeys to tuberculosis when brought to this country. The change of habitat and surroundings induce this predisposition. Perhaps we had better say that greater exposure to the germ coupled with impaired health from unnatural living brings about this mortality.

Pneumonia stands third in the list of causes of death. It is rare that I save a case of pheumonia either in adult or child among the colored, and an inspection of the mortuary records brings out a great disparity between the two races. Here is a table of the deaths from pneumonia since 1884.

YEAR.		*1884*	*1885*	*1886*	*1887*	*1888*	*1889*	*1890*	*1891*	*1892*	Total.
Pneumonia	W	17	9	16	15	22	18	7	23	20	147
	C	33	37	74	41	48	46	47	52	52	430

Here in nine years we have had 147 cases of pneumonia among the whites and 430 among the colored, in other words one white dies to three colored. The Census states, "The comparative excess of mortality from pneumonia in the colored race in the South has been known for a long time." The disease with them rapidly assumes a general infection; there is a high temperature, typhoid symptoms, singultus, unconsciousness, and death. Cases which recover are apt to succumb later to tuberculosis.

Here are the figures put down to bronchitis and capillary bronchitis:

YEAR.		1884	1885	1886	1887	1888	1889	1890	1891	1892	Total.
Bronchitis	W	5	3	2	3	3	1	5	7	4	33
	C	10	6	15	4	12	11	17	13	20	108
Capillary Bronchitis	W	0	4	2	3	2	2	2	2	3	20
	C	0	5	7	2	1	2	4	5	9	35

Bronchitis is not common with us, and the doubt in the diagnosis is to be considered. The Tenth Census states it causes a greater proportion of deaths in the white (17.3) than in the colored (12.8). It is, however, a small factor in the general mortality here in the South.

I give here a strange pathological table which shows the difficulty we sometimes labor under from improper diagnosis, or rather no diagnosis at all. There is an immense return, for example, under "anasarca" which is simply a symptom, and may result from heart, liver, or kidney trouble, and even other troubles. Again, "ascites" is usually a symptom of hepatic cirrhosis, but may occur from other abdominal conditions as well as heart and kidney troubles. "Cardiac dropsy" gives us no idea of the real condition present. To offset this I have added the cases of Bright's disease, hepatic cirrhosis, and heart disease, including under the latter term all specified diagnoses of heart trouble. Although the figures here reduce somewhat the great disparity from "anasarca," "ascites," and "cardiac dropsy," it is very evident that the colored are still largely in excess of the whites in cardiac and renal diseases.

According to this table hepatic cirrhosis is more frequent among the whites, yet if we combine the figures with those of ascites, the colored are in excess. Again it is the heart troubles which add mostly to the mortality, and while even here the negro mortality exceeds that of the whites, still it is in Bright's disease that we find the greatest disparity, and greater still if we include a certain proportion of the cases

under "anasarca," which we are justified in doing, I think. Whichever way we turn the pathological horizon remains the same, the colored looming up ever on the darker side of the picture.

YEAR.		*1884*	*1885*	*1886*	*1887*	*1888*	*1889*	*1890*	*1891*	*1892*	Total.
Anasarca	W	7	3	11	7	1	2	2	1	1	35
	C	30	28	28	36	15	12	17	21	20	207
Ascites	W	.	. .	. .	. .	. .	1	0	0	0	1
	C	.	. .	. .	2	. .	2	16	6	7	33
Cardiac dropsy	W	0	2	. .	. .	. .	. .	. .	0	0	2
	C	2	0	. .	3	. .	. .	. .	2	1	8
Bright's disease	W	5	5	5	5	4	10	13	6	12	65
	C	4	6	9	7	15	8	8	23	13	93
Hepatic cirrhosis	W	3	0	. .	3	4	5	4	2	0	21
	C	0	2	. .	1	1	0	1	1	0	6
Heart disease	W	24	14	25	25	20	2	23	19	32	184
	C	14	28	22	27	17	14	29	15	18	184

The Tenth Census states: "These figures confirm the statement just made that much of what thirty years ago was reported as dropsy is now reported as heart disease; and for this reason, as well as to permit of a comparison presently to be referred to, heart disease and dropsy are grouped together in the present study. They caused a greater proportion of deaths in the rural districts (59.7) than in the large cities (46.4), and a greater proportion in the colored (64.5) than in the white (56.1) . . . . . ."

In the Tenth Census Bright's disease is not considered separately but comes under "Diseases of the Urinary System and of the Male Organs of Generation" where the mortality appears less for the colored. (White, 19.2, colored, 9.6). I find no records in the Census of hepatic cirrhosis.

I give here a table showing the total deaths for white and colored under "Undefined" and "Death without Physician."

Year.		1884	1885	1886	1887	1888	1889	1890	1891	1892	Total.
Undefined . .	W	5	9	13	7	5	6	17	19	14	95
	C	37	70	82	94	81	133	139	100	143	879
Death without physician . .	W	13	7	14	15	7	10	20	23	9	118
	C	119	114	240	250	182	220	301	215	208	1849

This is another gloomy side to the picture. In the present state of the world there is no denying the fact that the poor cannot command the attention which the rich and the well-to-do can. However willing the physician may be to care for the sick poor the unsatisfactory conditions and surroundings in which they live, conditions which he is not able himself either by advice or moré tangible means to remedy, must detract from his interest in the case. Called to a patient in poverty and dirt he feels that before his services can avail, before he makes his diagnosis, prescribes, and gives his directions, the patient needs a clean bed and a warm room, pure air and suitable nourishment and attention, and directions properly carried out. These all failing he feels utterly helpless to treat the case. He can but make his diagnosis and prescribe, and go away.

Furthermore, there is apt to be among the masses of the colored an indifference, real or apparent only, on the part of the patient and family which must add to the physician's indifference and must be a damper to help from outside. You see it in the patient and you see it in the family, and even in the mother for her child. You are called to a sick negro and he will hardly turn over in bed to face you and answer you, and seems quite indifferent whether he answers your questions or not, and you may go away without knowing the real cause of your being sent for. This happens so often that you soon come to look upon it as a racial characteristic. This explains how often you meet neglected cases, cases of ugly wounds and ulcers, whose very loathsomeness and discomfort, not to say real pain, you imagine would compel them to seek advice and treatment. You see this in ven-

ereal troubles which are allowed to go on until irreparable damage has been done. For the same reason you rarely get a malignant growth in its beginning; it is only when it has gone so far that radical treatment is out of the question that they finally see the physician. A carcinoma of the breast is left until the axilla becomes involved and the violent pain finally compels the patient to seek aid. A phagedenic sore is allowed to reach a great size before it occurs to the poor patient that it had better be looked after. This explains how often the physician is sent for when the patient is moribund, how often a death-certificate is demanded of the Health Officer for cases which have never been seen by a physician. And here are the figures to speak for themselves, 95 whites with a certificate of "undefined" against 879 colored with the same blank certificate; and 118 whites dying without medical attention against 1,849 colored unattended, and in the last nine years, and in a population not exceeding 50,000, and with the whites between 5,000 and 10,000 in excess. And this indifference is largely due to an insensibility to pain as well as a lack of pride in physical well-being, pride in the possession of a complete body with all its faculties operative, a quality possessed by the higher order of man. This insensibility is seen in minor surgical operations, in the parturient woman, and in the neglected wounds and lesions, and the many little ills which the more sensitive would seek relief from. The loss of an eye or a member carries with it but little concern. And all this is but that fatalism which has come to them from the past.

In considering the high infant mortality I spoke of syphilis in its effects upon premature and still-births, and I shall now speak of the effects of the two venereal diseases upon the adult population. We shall never get any figures which can even approximately show us the real influence deathward of these troubles. That they are all-potent in the white race must be admitted, and their ravages among the colored become very real to the physician practicing among them. The figures which I have been able to obtain from our mortuary tables are too small to have any value. I give them, however, for what they are worth.

YEAR.		1884	1885	1886	1887	1888	1889	1890	1891	1892	Total.
Syphilis	W	2	1	0	0	0	1	1	1	0	6
	C	4	11	6	12	8	1	6	6	9	63
Urethral stricture	W	0	1	0	1	0	0	1	0	0	3
	C	0	0	1	0	0	1	0	1	0	3

It is the physician only who can trace the pathological lines leading to ill health and death whose course has been set, directly or indirectly, by these two diseases. They lie so much beneath the surface, cropping out in so many unforeseen ways, and at so many unexpected points, that the scientist is often at a loss how to draw his pathological relief-chart. There are so many deep lesions of nerve-centres, viscera, and blood vessels, which are the outcome of syphilis, contracted, perhaps years before, that the disease has a most potent influence in reducing the vital equation. And especially is this the case when there is a history of neglect and intemperance, factors which enter so largely into the disease among the colored. As a consequence we see all these stages in virulent form; mixed and phagedenic sores primarily, followed by severe secondaries, tubercular and pustular syphilides, violent throat symptoms, iritis, and keratitis. Its tendency among the women to produce abortion I have already mentioned. I have not seen anything to compare with it among the whites. And we see here not only the prospective loss of life but all the dangers to the woman of the miscarriage itself.

The congenital form is so virulent that most of the infants do not reach term. And with all these flagrant examples of its lethality, there is probably as large a class dying of other diseases where the vitality and the resistive power have been so undermined by syphilis that they have succombed to a strain which they could otherwise have borne.

The large majority of the cases of pyelo-nephritis and cystitis can be traced to the infection from gonorrhoea, and with

women the serious complications of salpingitis and pelvic peritonitis are traceable to the same cause. Both these factors must influence the colored, for this disease is always serious with them, both from predisposition and the most flagrant carelessness. I have never among the whites seen such neglected cases of old strictures where urethral abscesses and fistulæ have formed, and where they have been content to go along without interference until, perhaps, extravasation of urine has compelled them at the eleventh hour to seek surgical help. One of these cases I have just operated upon and with fatal result, and hardly a month has passed since I was called to a negro whom I found lying upon a dirty floor dying from an extravasation of urine which had taken place several days before, and for whom nothing had been done or any surgical aid sought, although probably twenty negroes in the settlement knew of his condition. I mention this as showing that apathy, that indifference to make a struggle for life, which is such a strong racial trait.

Of the returns from venereal diseases the tenth census states: "In those parts of the country where the distinctions are made between white and colored, and Irish and German parentage, the proportions are, colored, 3.0, whites, 1.7, Irish, 1.4, and German, 1.3 per 1000 deaths from known causes." The returns from alcoholism and venereal diseases are always very imperfect, and I give these figures for what they are worth.

The negro once could boast of his unsusceptibility to malaria and live secure in regions fatal to the white man. But this exemption has been growing less and less complete, and to-day the colored mortality from malarial and miasmatic diseases is very much greater than it once was. The reasons for this are various. In the first place a large part of this mortality is from the mixed element which is more susceptible than the pure negro by virtue of the white admixture. This is self-evident. In the second place, a less resistive power naturally follows a less healthy physique. In the third place, in the so-called malarial and miasmatic diseases an

enteric factor is apt at times to be an important element, an element to which the colored are very susceptible, and which is very fatal to them. This has been plainly shown by statistics collected during the war among the colored troops.

The etiology of our prevalent fevers included under the terms malarial and miasmatic is largely a jumble of mere theories and opinions. There are certain ones which seem to be purely malarial, as we understand the term ; others seem to be larval forms, masked by other elements vaguely called climatic ; and others where a distinct enteric or typhoid character is shown. We call them typho-malarial, a convenient term, but one which prompts to laziness in our efforts to differentiate more closely. All these fevers from the simple continued fever up to the severer forms of the malarial remittent, of the bilious and hemorrhagic types, are constantly met with among the colored. My experience has been that the simple continued fevers, without any complications, run a protracted course and are hard to break, while the severer malarial remittents and the typho-malarial are very fatal. Granted that the pure negro bears, comparatively speaking, a charmed life in rice fields and uncultivated districts very fatal to the white man, his much greater exposure swells his death list, and this is the important point. Typhoid fever proper is a rare disease with us, comparatively speaking, and when it occurs generally assumes a larval form, masked and modified in one way or another by our climatic influences. To these fevers the negro rapidly succumbs.

This year we have had more typhoid fever and remittent fevers of various types than has ever been known in Savannah, and a reference to our mortuary tables will show that, taking all forms of fever into consideration, the colored mortality is greater.

YEAR.		*1884*	*1885*	*1886*	*1887*	*1888*	*1889*	*1890*	*1891*	*1892*	Total.
Bilious malarial . .	W	.	. .	. .	1	1	0	. .	1	. .	3
	C	.	. .	. .	4	1	1	. .	0	. .	6
Congestive malarial	W	15	10	16	9	6	11	16	10	6	94
	C	4	2	12	3	3	4	7	7	8	50
Typho-malarial . .	W	1	5	4	9	3	1	12	11	5	51
	C	3	7	9	10	2	9	15	10	24	89
Remittent malarial	W	12	5	16	8	5	10	1	1	12	70
	C	18	3	41	13	12	14	14	0	19	134
Typhoid fever . . .	W	8	4	11	10	8	4	17	5	21	88
	C	11	4	11	0	4	6	9	12	11	68
Intermittent malar.	W	2	0	. .	. .	2	2	1	3	. .	10
	C	5	1	. .	. .	4	0	0	1	. .	11
Malarial fever . . .	W	5	6	. .	6	. .	. .	10	7	. .	34
	C	9	11	. .	22	. .	. .	10	8	. .	60
Hæmorrhagic mala	W	.	. .	. .	. .	. .	. .	. .	1	1	2
	C	.	. .	. .	. .	. .	. .	. .	0	0	0
Continued malarial	W	.	0	. .	5	1	3	. .	. .	. .	9
	C	.	1	. .	9	4	2	. .	. .	. .	16
Gastric fever . . .	W	.	1	. .	1	. .	1	. .	. .	1	4
	C	.	0	. .	0	. .	0	. .	. .	0	0
Catarrhal fever . .	W	1	. .	. .	0	. .	. .	. .	. .	. .	0
	C	1	. .	. .	1	. .	.	. .	. .	. .	2

This increased susceptibility to our continued types of fever, as well as yellow fever, is a significant and interesting point and will be brought out more fully when I show the Consolidated Mortuary Record of Savannah from 1854 to 1883 inclusive. The above table also shows the uncertain state of our nosology and the elasticity of our nomenclature. If you can exclude typhoid fever you may call our continued types of fever anything you please.

The tenth census states as to typhoid fever, "as causing a somewhat greater proportion of deaths among the whites than among the blacks, the figures being, for the whites, 33.9 and

for the colored 31.7 per 1,000 deaths from specified causes. Up to the age of 15 the number of deaths from this cause is proportionately greater among the colored." And as to malarial fevers: "The proportion of deaths from these causes is decidedly greater in the colored (48 3) than in the whites (30.7), but this rule by no means holds good in all the grand groups. The excess in the proportion of deaths from these causes among the colored population occurs throughout all the groups of ages."

As to the exanthematic fevers, I have already mentioned the high mortality from measles among the colored children. We have a history of its malignancy in the Sandwich Islands, where a large number of the population were swept away.

It has long been recognized that the negro is peculiarly susceptible to smallpox and that the mortality is high. In a small epidemic in 1891, 44 cases were reported to the Health Officer, of which 4 were white and 40 were negroes. There was one death among the whites and 21 among the colored, that is, a mortality of 50 per cent. Two of these were found dead and seven *in extremis*, showing their usual carelessness and indifference. Smallpox was introduced into Savannah in 1865, 1866, 1867, 1875, 1876, 1882, 1884 and 1885, during all of which times the disease went hard with the negroes, and they who recovered were severely pitted. In vaccinating them with lymph from the calf many suffered from severe sores which were long in healing. As I have stated the colored are not susceptible to scarlatina, or the allied poison of diphtheria. These diseases, moreover, are not common with us.

Cholera was brought into Savannah in 1866, resulting in 85 deaths among the whites and 211 deaths among the colored. In 1867 there were 12 deaths from this disease among the whites and 17 among the colored; and in 1868, 13 deaths among the whites and 18 among the colored.

It is an interesting and significant fact that prior to emancipation the negro was quite exempt from yellow fever. In 1854 there were in Savannah, from this disease 625 deaths among the whites and only 10 deaths among the colored, while in 1876 there were 771 deaths among the whites and 125 deaths

among the colored. In other words, in 1854 about 5 per cent. of whites died of yellow fever, and only one-eighth of one per cent. of colored, while in 1876 about 4½ per cent. of whites died and very nearly one per cent. of colored. Of course these figures are only approximately correct as no account has been taken of the exodus from the city at these times of peril. These figures will be seen in a table giving the consolidated mortuary record of Savannah from 1854 to 1886 inclusive, which I shall introduce later, and which also shows the better physical status of the negro before emancipation.

The great strides which have been made in recent years in the etiology of disease through bacteriological research have thrown much light upon susceptibility to disease, the predisposition to certain morbid processes which some have more than others. And this investigation helps as greatly in the study of racial tendencies. In Europe where so much has been done in this way geographical areas and nations living under their different conditions can be mapped out on pathological lines. This same work is being done in America, and it cannot be very long before the colored race and its relations to the inimical factors which produce disease and death, will be better understood.

The susceptibility of the colored to tuberculosis is now generally recognized; in other words they succumb to the bacillus tuberculosis. To pneumonia, another germ disease, they also quickly succumb, and on this line I have but to repeat what I have already said in treating of the different diseases.

Recent researches are showing us that the various pathological processes in the production of tumors, and especially the malignant growths, are the direct outcome of minute organic forms, certain fungi and protozoa, and it cannot be long before we shall know definitely the proximate causes of the many varieties of carcinoma and sarcoma, diseases which are, according to English statistics, on the increase. The figures at my disposal are too small to have any value; so far as they go they show that the whites are still more liable to cancer than the colored. The tenth census states: "In males the proportion of deaths per 100,000 of living population is, for

the whites 20.54, and for the colored 5.85 ; in the females the proportions are, for the whites 35.44, and for the colored 19.32." From all I can learn, however, cancer is more common now than before emancipation when the vital equation of the race was better. The cases I meet are very rapid, especially of the *cervix uteri*. The most malignant sarcoma I have ever seen was in a mulatto. Of osteo-sarcoma I have seen but four cases, three negroes and one white. Of the two cases of malignant lymphoma I recall, one was white and one colored.

It is an interesting fact that just across the border from malignancy there are certain tumors to which the negro is very liable. Of these the fibromata are especially noticeable ; the uterine fibroids, fibroma molluscum of the skin, the tendency to keloid tissue, all show this great fibrous-tissue proliferation. I have seen uterine fibroids of enormous size, and especially among the mulattoes. I am constantly called upon to remove fibromas of the lobule of the ear caused by the irritation of the ear ring. Fibromata of the neck are common, starting from enlarged lymphatic glands, a frequent trouble with them.

The formation of keloid tissue and hypertrophied scar-tissue seems naturally to follow this connective-tissue proliferation. I have seen it mostly on the breast and neck following operations. Erythema nodosum seems but the first step in the pathological process producing fibroma moluscum. I have seen but two cases of this trouble and they were both colored.

On this same line I may mention arterio-sclerosis which I believe to be a not uncommon disease among the colored, although rarely recognized as such. We get but few chances for post-mortems which would help us so much in our pathological tables. A further and more pronounced condition, atheroma, is constantly found. I have recently had a most remarkable case of this kind in a negro about fifty-five years old who looked seventy, and whose brachial artery was subcutaneous and outside the deep fascia from the axilla to the elbow. By pinching up the artery with the finger all circulation in the arm was controlled. Its atheromatous condi-

tion was very evident. The large contingent put down as dropsy, with heart and kidney complications, has probably in many cases an arterio-sclerosis basis. In my own practice I have seen more cases of aneurism among the colored than among the whites. Dr. A. Corre in his voluminous work (Traité clinique des Maladies des Pays Chands, Paris, 1887), writes, p. 463, in a foot note, "nous avons été surpris du grand nombre d'anévrysmes artériels qu'on rencontre chez les noirs et les mulâtres." Cerebral apoplexy and paralysis have a bearing here and I have drawn up the following table showing the deaths from aneurism, apoplexy, and paralysis.

YEAR.		*1884*	*1885*	*1886*	*1887*	*1888*	*1889*	*1890*	*1891*	*1892*	Total.
Aneurism	W	1	0	0	0	2	0	0	2	2	7
	C	1	2	0	0	1	1	2	1	1	9
Apoplexy	W	8	4	4	4	6	5	3	9	3	46
	C	4	8	11	2	2	8	3	9	5	52
Paralysis	W	15	6	14	10	13	12	15	9	15	109
	C	15	9	12	11	20	11	7	17	11	113

These figures are quite too small to draw any conclusions from. The colored at least keep well apace with the whites.

According to the tenth census the deaths from apoplexy and paralysis are greater among the whites (35.1) than among the colored (15.9). I have more confidence in my own figures.

The negro shows a tendency to suppuration ; in other words, he has less resistive power against those purifacient cocci which cause the ordinary suppurations in the body. On the slightest provocation he has glandular swellings followed by abscesses in inguinal, cervical, and axillary glands, acute abscess of the tonsil, onychia, and suppurative foci generally. The tubercular syphilide is frequently followed by a pustular one ; variola produces marked suppuration and pitting. Cuts and contusions often result in suppuration. All this shows a

lack of resistive power against certain germs, especially the staphylococcus, and is another minus factor in lowering the vital equation. While not directly causing death, it may do so indirectly and appear in the mortuary records under other headings. Corre, above quoted, also mentions this predisposition, having met with many cases of cold abscess and suppurative lymphatic glands.* In treating of hepatic abscess he states that while more common with Europeans the relative mortality is greater among the negroes. He states further that the negro, when in Africa and not transported, enjoys considerable immunity against hepatitis, but that outside his own country, even if in a similar climate, he loses this immunity and shows a mortality equal to, or greater than, that of the European.†

I have never seen a case of *delirium tremens* in the negro. I think this is easily explained. We usually find *delirium tremens* in those of tough fibre who can stand that heavy and prolonged drinking necessary to develop the disease. The negro cannot stand this heavy and prolonged drinking. He is soon done for and becomes so overcome by the drug that he must let up for a while ; or he becomes disorderly and commits some violence which sends him to the barracks and the chain-gang, where his stomach has rest and where he is enabled to pick up again. The evil effects of alcohol then are seen in acts of violence, in the inflammatory troubles which follow exposure while under the influence of the drug, and those congestions and inflammations of the thoracic and abdominal viscera which can be traced directly to alcohol in all its forms.

Dr. Billings writes : "The proportion in those parts of the country in which the colored distinction is made is much greater among the whites than among the colored, and where the distinction of parentage is made, it is much greater among the Irish than among the Germans, the figures being for the Irish 6.7, for the Germans 2.7, and for the colored .7 per 1,000 deaths from known causes. A large proportion of the deaths

* Op. Cit., p. 466.

† Op. cit., p. 797.

reported as due to alcoholism occur in connection with delirium tremens and this form of disease is rare in the colored race."*

To the physician in active practice, however, it is not necessary to see alcoholism in the form of delirium tremens to realize its evil effects. It is seen in so many side channels as inciting to congestions, catarrhal inflammations, fibrous proliferation, and a general lowering of the vital powers. It often turns the scale when the patient is fighting for his life. It diminishes his working capacity and mental acumen. These evil effects are but too plainly seen among the colored, so that a review of the deaths from delirium tremens can in no way show the extent of the evil. The large number of cases of "dropsy" and "heart disease," and evident arterio-sclerosis, is probably in a measure due to alcoholism. It must be remembered, too, that it is only the cheaper spirits they can buy, largely composed of methyl alcohol. Alcoholism directly and indirectly has always been an immense factor in the mortality of the lower classes. It played havoc among the American Indians, and the same story comes to us from India.

The question of insanity is an interesting one. In searching through the records at the Ordinary's office, I find there have been 84 cases of insanity among the whites and 133 among the colored since 1879. Through the courtesy of Dr. T. O. Powell, Superintendent of the State Lunatic Asylum at Milledgeville, I have some interesting figures bearing on the subject. In 1860 there were only 44 insane negroes in the State in a population of 465,698, or one insane negro to every 10,584. The Census of 1870 showed 129 insane negroes in a population of 545,142, or one colored insane to 4,225. The census of 1880 gave 411 colored insane, or one to 1,764 of the population.

All this shows a great increase in the liability to insanity, and while it is still more frequent among the whites, the rate at which the colored have increased in this direction promises to outstrip the whites at no very distant day. And this is to be expected when we consider the greater strain of to-day brought to bear upon them, the evil influences of syphilis,

* Vol. xii, p. 797.

alcoholism, and other irregularities. The cases I have seen have been mostly acute mania, of a religious type. Dr. Powell states that he has never seen a case of paresis in the negro. I have seen several cases of epileptic imbecility among them. Hysteria is common among the women, and the most typical cases of hystero-epilepsy I have ever seen, three in all, if my memory serves me, were among the colored. The emotional side of the negro is pronounced; you see it in all their gatherings, especially the camp-meetings, where many work themselves up into a religious frenzy.

Speaking of miscegenation I wrote in my first paper: It would be an interesting point to know the percentage of this mixed-element to the pure African. I am persuaded that it is much larger than generally believed. The census unfortunately has made no distinction in the enumeration. It is, however, a distinction which should be made, and any correct returns would point to many significant tendencies, and be a *point d'appui* for our argument. This mixed-element indicates the fusion and assimilation going on. That it bears the same social stigma as the darker color shows that the barrier between the races is a social but not a physiological one, for underneath this barrier miscegenation goes on through many channels. This new product is a large one though it is largely unstable.

Miscegenation will go on in the future as it has gone on in the past. Its illegality will be no bar to it, though the process of fusion may be retarded. To my mind race predjudice will not be in the years to come what it has been or what it now is. Time alone, throwing the days of bondage further back into the past, will in itself modify and soften these feelings of race, especially when, by the gradual fusion, the color will become lighter and the mixed-element will exhibit qualities allying it more and more to the Caucasian. It will not be in our day, of course, nor in the next generation; it may take centuries, but it will come."

The question whether the mere mixing of the races in itself results in an unstable product is one which I have not been able to answer to my own satisfaction. My

opinion is that this instability is largely the direct inheritance of a weakness and degeneracy of one or both parents, as naturally follows the laws of reproduction and inheritance. Still there seems to be a factor outside of this, a factor dependent upon miscegenation itself. The mixing of different nationalities of the white race often appears to strengthen the new products, but the ethnic chasm which separates the Caucasian from the African is too wide for nature to bridge successfully. The bridge is but temporary and gives way to the strain it must eventually bear. Whatever the true explanation may be, the fact remains that this mixed-element is an unstable one with a high rate of mortality.

In the six years which have gone by since I wrote the above I am still more convinced of the poor vital equation of this mixed element. Their susceptibility to tuberculosis is certainly very great, and I have attempted to show what a large factor this is in the general mortality. We see it in their children, in the lowered prolificness among the women, in the greater tendency to dystocia, in the frequency of diseases of the uterus and adnexa. And in spite of the fact that it represents a better class socially, who lead better lives and live altogether more hygienically. I have noticed this in their churches, and social and political organizations. The congregations of their episcopal churches are largely of the lighter color; they have more social pride, and represent altogether a better living class, and yet withal their vitality is poor.

This element, I firmly believe, is greatly on the increase. Attempts by the census to show the proportion of pure blacks to all the shades of admixture with white blood have signally failed, and we must wait another decade before we can have any reliable figures on this point. For some time I have looked upon this miscegenation as a reducing agent, chemically speaking; it withdraws vitality from the pure negro and produces a new compound which is even less stable.

Though not bearing directly upon the question of vitality it may be interesting to compare the deaths of the two races from accidents and violence. Here are the figures for Savannah at least:

YEAR.		*1884*	*1885*	*1886*	*1887*	*1888*	*1889*	*1890*	*1891*	*1892*	Total.
Death from accident and violence	W	9	21	6	18	8	31	37	32	31	193
	C	16	19	17	19	18	33	29	29	33	213

Though there is no great disparity the figures are in favor of the whites. The tenth census states: "In that part of the country in which the color distinction is made they caused among the colored 67.6 and among the whites 43.8 per 1,000 from all deaths from specified causes."

I have thus far attempted to show the various pathological lines by which this high mortality among the colored is reached. Of its incompleteness I am only too painfully aware, for we have not yet the figures which can enable us to draw very sharp lines. The attempt has been made in the tenth census, and however much we may admire the evidence of work and care in the elaborate tables and maps, we feel that much is still lacking, and especially so on the question before us. I believe that a collective investigation among the physicians practicing in large colored communities would be the best method at our command at present, and it is this belief which has prompted me to give my own experience in a typical southern city of a sufficient population to draw fairly reliable conclusions from. This method seems to me less liable to error than the more superficial view of a large geographical area, with many gaps to be filled in.

I introduce here a table I gave in my first paper of the consolidated mortuary record of Savannah from 1854 to 1886 inclusive, which, with some allowances, gives a fair idea of the state of affairs in our city.

CONSOLIDATED MORTUARY RECORD OF SAVANNAH, GA., FROM 1854 TO 1886 INCLUSIVE.

From 1854 to 1870, and from 1870 to 1879, no reliable census is attainable; consequently I have estimated the increase of population *pro rata* yearly during said interims, and have computed the annual ratio of deaths per 1,000 of population upon this status. Although not numerically correct, the estimates are nearly enough so to give valuable statistical information.

This table proves conclusively that prior to the freedom of the African race in the United States their death ratio was smaller than that of the white race.

Year.	Population.		No. of Deaths.		Ratio per 1000 of Population.	
	Whites.	Blacks.	Whites.	Blacks.	Whites.	Blacks.
*1854 . .	12,468	8,961	1,221	308	97.9	34.3
1855 .	Population—Whites increased yearly upon an estimated gain of one hundred and fifty-four (154).	Population—Blacks increased yearly upon an estimated gain of two hundred and sixty-nine (269).	433	292	34.3	31.6
1856 .			466	297	36.4	31.2
1857 .			376	264	29.0	27.0
*1858 .			592	262	45.2	26.1
1859 .			430	273	32.4	26.5
1860 .			474	282	35.3	26.7
*1861 .			563	269	41.5	24.8
1862 .			555	372	40.4	33.5
1863 .			459	389	33.7	34.2
*1864 .			747	446	53.3	38.3
†*1865 .			1,202	819	84.8	68.9
‡†1866 .			530	912	37.0	75.0
‡†1867 .			476	594	32.8	47.3
‡*1868 .			498	581	34.0	45.8
*1869 .			423	429	28.6	33.1

Year.	Population.		No. of Deaths.		Ratio per 1000 of Population.	
	Whites.	Blacks.	Whites.	Blacks.	Whites.	Blacks.
1870 . .	14,938	13,217	450	576	30.1	43.5
1871 .	Population—Whites inc. yearly upon an est. gain of two hundred and eighty-four (284).	Population—Blacks inc. yearly upon an est. gain of two hundred and sixteen (216).	526	606	34.4	45.1
1872 .			519	636	33.4	46.5
1873 .			558	789	34.0	56.1
1874 .			394	642	24.5	45.5
†1875 .			394	602	24.0	42.1
†*1876 .			1,265	984	76.0	67.8
†*1877 .			375	623	22.1	42.2
1878 .			362	626	21.0	41.8
1879 . .	17,493	15,163	416	686	23.7	45.1
1880 . .	18,229	15,019	462	885	25.3	58.8
1881 . .	19,114	15,765	557	903	29.1	57.2
1882 . .	20,514	16,819	375	740	18.2	43.9
1883 . .	23,839	16,652	488	659	20.4	39.5
1884 . .	25,362	19,150	469	703	17.9	36.7
1885 . .	25,720	19,111	333	659	13.7	35.4
1886 . .	26,675	19,111	458	953	17.1	49.8

*Yellow fever 1854—Deaths, whites 625, blacks 10. *1858—Deaths, whites 112, blacks 2. *1861—Deaths, whites 4. *1864—Deaths, whites 14. *1865—Deaths, whites 1. *1868—Deaths, whites 1. *1869—Deaths, whites 1. *1876—Deaths, whites 771, blacks 125. *1877—Deaths—whites 4. †Small pox introduced by United States troops 1865, 1866, 1867. †1875, 1876, 1877, †1882—One case. †1884—Two cases. †1885—One case. No accurate account can be given as to deaths; it was very heavy in 1865 and 1866. ‡Cholera brought from New York by United States troops. 1866—Deaths, whites 85, blacks 211. ‡1867—Deaths, whites 12, blacks 17. ‡1868—Deaths, whites 13, blacks 18.

I am indebted to compilation of our honored townsman, Dr. W. Duncan, for tabular statement of deaths from 1855 to 1869 inclusive.

J. T. McFARLAND, M. D., Health Officer.

In this table we find that from 1854 to 1863 more whites died proportionately than colored. Then from 1864 to 1876 the white mortality was still in excess of the colored. The year 1866, however, was the turning point, for with the exception of 1876, the year of the yellow fever, the colored have greatly exceeded the whites in mortality.

From 1880 the returns show that twice as many colored as whites die in proportion to the population. Some years show an even greater mortality. In 1880, in the ratio per 1000 of population, the figures stand 25.3 for the whites and 58.8 for the colored; in 1882, 18.2 for the whites, and 43.9 for the colored; in 1884, 17.9 for the whites, and 36.7 for the colored; in 1885, 13.7 for the whites, and 35.4 for the colored; in 1886, 17.1 for the whites and 49.8 for the colored. This table shows conclusively, for Savannah at least, that prior to emancipation the death rate of the colored was less than that of the whites, but that since their freedom their mortality has greatly exceeded that of the whites. It would be indeed valuable for our subject could we get similarly prepared tables from other parts of the country.

To this I now add a table which continues the figures up to 1892 inclusive, which shows the same high rate of mortality among the colored, a mortality, which, making all due allowance for error, about doubles that of the whites. I omit, however, the estimated population and the ratio per 1,000 deduced from it as the figures are largely guess-work. It is sufficient to remember that the population is now about 45,000, and that the whites exceed the colored by about 5,000.

Year.	No. of Deaths.	
	White.	Colored.
1887	458	798
1888	366	665
1889	384	685
1890	479	870
1891	464	746
1892	468	834

In my first paper, in conjunction with the above consolidated mortuary record of Savannah, I composed the returns I was able to get from Charleston, New Orleans, Richmond, Nashville, Chattanooga, and Knoxville, and I found results tallying fairly well with those of our own city. I give here a table showing the relative death rate in six cities, where there is a sufficient colored population to make a comparison, for the census year 1879–80.

Cities.		Deaths per 1000 of living population.
Louisville . .	W	20.04
	C	34.75
Washington .	W	17.80
	C	35.45
Richmond . .	W	19.12
	C	31.97
Baltimore . .	W	22.71
	C	37.61
New Orleans .	W	22.41
	C	35.61
Charleston .	W	23.78
	C	45.00

I have not been able to obtain a sufficient number of reports from other cities to carry out, as it should be done, a comparative statement of the mortality records, nor does it come within the scope of this paper to do so. It is sufficient for my argument that they all bear testimony to a large mortality among the colored and greatly in excess of the whites. Of course I am aware that the mortality falls outside the

cities ; and the reasons for this are quite too apparent that I should elaborate them here. The one important point in my argument is, that the negro cannot stand the sharp competition in the cities, that when thrown directly in the struggle for existence with the white race he cannot hold his ground, that the more densely populated the country becomes and the fiercer the struggle, the more he must lose ground, and that his greater mortality shows us the extent of his defeat.

Having shown, as I hope, this greater mortality and the various ways by which it is brought about, it will be interesting to see how this accords with the teachings of ethnology and biology which treat the subject from the standpoint of the naturalist. It is only in this way we discover the relationships of organic forms from the lowest to the highest, and the laws governing the survival and death, the increase and decrease of species and races, with man as a part of the animal kingdom.

And first and foremost, the inferiority of the negro as compared with the Caucasian.

It would hardly seem necessary to dwell at any length upon the conditions which stamp the African race as one greatly inferior to our own. When writers like Mr. Tourgée ignore this fact, and not only ignore it but seem to put the two races on an equality, it is not necessary to discuss the question with him ; but for the sake of our argument we shall indicate briefly the salient points of difference between the Caucasian and the African as taught us by ethnology and comparative anatomy.

The pure negro is the representative of a race whose natural habitat is the African mainland. Though spread over a large area it shows a greater uniformity in physique and moral type than is to be found in the other great divisions of mankind. To the ethnologist it marks a type the lowest in the scale of humanity.

A. H. Keane gives us the following points as indicating the low type and nearer approach in body to the quadrumana or anthropoid apes :

"(1) The abnormal length of the arm, which, in the erect position, sometimes reaches the knee-pan, and which, on an

average, exceeds that of the Caucasian by about two inches; (2) prognathism, or projection of the jaws (index number of facial angle about 70, as compared with the Caucasian, 82); (3) weight of brain, as indicating cranial capacity, 35 onnces (highest gorilla 20, average European 45); (4) full black eye with black iris and yellowish sclerotic coat, a very marked feature; (5) short, flat snub nose, deeply depressed at the base or frontal suture, broad at extremity, with dilated nostrils and concave ridge; (6) thick protruding lips, plainly showing the inner red surface. (7) very large zygomatic arches—high and prominent cheek-bones; (8) exceedingly thick cranium, enabling the negro to butt with the head and resist blows which would inevitably break any ordinary European's skull; (9) correspondingly weak lower limbs, terminating in a broad flat foot with low instep, divergent and somewhat prehensile great toe, and heel projecting backwards ('lark heel'); (10) complexion deep brown or blackish, and in some cases even distinctly black, due not to any special pigment, as is often supposed, but merely to the greater abundance of the coloring matter in the Malpighian mucous membrane between the inner or true skin and the epidermis or scarf skin; (11) short black hair, eccentrically elliptical or almost flat in section, and distinctly woolly, not merely frizzly, as Richard supposed on insufficient evidence; (12) thick epidermis, cool, soft, and velvety to the touch, mostly hairless, * * *; (13) frame of medium height, thrown somewhat out of the perpendicular by the shape of the pelvis, the spine, the backward projection of the head, and the whole anatomical structure; (14) the cranial sutures, which close much earlier in the negro than in other races. *

These anatomical characteristics are well known to every careful observer; they mark a distinct race of mankind and show conclusively an inferior type. The natural habitat of the race is in itself indicative of its inferiority, for whatever Egypt may have been in the past, and history certainly points to a high order of civilization ages before the Christian era, Africa for centuries has been the home of the savage. It is

* Encyclopædia Brittanica, Article "Negro."

the cranial and facial characteristics which have the direct bearing upon the points at issue. The prognathism, the facial angle, the weight of the brain, the thickness of the skull, and the early closure of the cranial sutures, all point to a lower intellectuality and an inferior nervous system.

The negro infant starts apparently with a great advantage over the white child; it is more precocious in every way, and maturity comes sooner. But this rapid growth soon reaches the end of its tether, and at a time when the negro has attained its full growth, the white child is but beginning to develop qualities which in time advance it to a point unattainable by its less fortunate rival. Even when educated up to a certain point by the efforts of, and association with, a higher race, the mind is in a condition of unstable equlibrium which reverts in time back to its original level when the civilizing influences have been withdrawn. Throughout the animal world whenever artificial conditions have been brought to bear to produce results different from those which nature attains by her slow methods, the new products when left to themselves fall back to their original starting points, or but little in advance of them. It will be like the stone of Sisyphus. In the two centuries and a half of association with the Caucasian the race in certain directions has been much benefited by the higher civilization. If these associations were to be suddenly and completely cut off, and the race were to be left to its own resources, its future would be a retrogression rather than an advance.

In this connection let me quote from Sir Spencer St. John, a most impartial and moderate critic, who, in his "Hayti or the Black Republic,"* gives us a dismal picture of the state of affairs in that unfortunate country. I am glad to find my own views substantiated by so good an authority.

"The vexed question as to the position held by the negroes in the great scheme of nature was continuously brought before us whilst I lived in Hayti, and I could not but regret to find that the greater my experience the less I thought of the capa-

* Hayti or The Black Republic. By Sir Spencer St. John, K. C. M. G., New York, 1889.

city of the negro to hold an independent position. As long as he is influenced by contact with the white man, as in the southern portion of the United States, he gets on very well. But place him free from all such influence, as in Hayti, and he shows no signs of improvement; on the contrary he is gradually retrograding to the African tribal customs, and without exterior pressure will fall into the state of the inhabitants of the Congo. If this were only my own opinion, I should hesitate to express it so positively, but I have found no dissident voice amongst experienced residents since I first went to Hayti in January, 1863.

"I now agree with those who deny that the negro could ever originate a civilization, and that with the best of educations he remains an inferior type of man. He has as yet shown himself totally unfitted for self government and incapable as a people to make any progress whatever. To judge the negro fairly one must live a considerable time in their midst, and not be lead away by the theory that all races are capable of equal advance in civilization." p. 134.

I am speaking now of course of the race without any admixture of white blood; with it the problem becomes a different one; the intellectual level rises, and the more this element enters into the combination the nearer the new product approaches the Caucasian. We may meet with the intellect of an Alexander Dumas, or Dumas, fils, though I think the product a rare one. It is in the large mixed-element that we find examples of those who have risen above the multitude of their race and have shown qualities which ally them closer to the superior race. To writers like Mr. Tourgée this factor of miscegenation does not enter at all into their calculations. They speak of whites and blacks as though it were a question of color only, with a sharp color line separating the two races, a mere difference in the amount of pigment in the Malpighian layer. One would think from their treatment of the subject that equal political rights and equality before the law meant equality moral, spiritual and intellectual. They lump together the entire colored population as a homogeneous mass to be measured by one standard. They bring forward ex-

amples of colored men who have attained considerable reputation, and have shown, perhaps, fine mental parts, to show the beneficial influences of education and civilization upon the African, and the possibilities of the race, and ignore the influence of the white admixture, and the credit due thereto.

And with this evident inferiority what can we learn further from biology?

A deterioration in physique may be looked upon as the natural result of the many influences at work arising from the transporting of the race to a foreign soil to be thrown into the struggle for existence against a superior race, a struggle which can have no ultimate issue but defeat, and by defeat I mean an inability to maintain the distinctive characteristics of the race. The struggle will be a slow process of fusion by which the weak and unstable elements will disappear while that which has any permanency will become so blended with the dominant race as to lose its individuality. Of the stable and the unstable the latter is by far the greater; its instability can be measured by the physical degeneracy. Even to-day to call the colored race the African race is something of a misnomer because it has undergone many modifications. A change in language, in soil, and in climate, a change of surroundings and associations are potent influences to eventually destroy the original African traits. This struggle may, perhaps, be better described as a process of assimilation by which the elements ill-adapted to the growth of the dominant race are thrown off, while that which is assimilable becomes gradually absorbed into the main growth.

Let us glance a little more minutely into these factors of change and decay. The change of habitat alone, a change of soil and climate, has a certain influence. Man, like the animals and plants, bears the stamps of geographical areas. A race indigenous to a certain country acquires through many generations characteristics the formation of which can be traced to climatic and telluric causes. One of the most interesting departments of biology is the study of the geographical distribution of animals and plants; and man is no exception, for in him, too, we can trace the influences of the ground he

treads and the air he breathes. And when man is removed from his home to a distant country, and is brought under different climatic and telluric conditions, he feels the change in proportion as the new environment differs from the old. Nature at once goes to work to adapt the new-comer to his new surroundings. The greater the change the harder the process of adaptability and the greater the waste and the loss of life. The medical histories of wars in distant climes in which Europeans have figured show that the loss of life from a new environment has often equalled, if it has not exceeded, that from the casualties of war. The Esquimaux can as little live in the tropics as the Hottentot in the polar region.*

Now while the change of the African to America has been more in longitude than in latitude it must still have an influence in modifying the race. The negro without any other modifying influences would be a different man five hundred years hence from the one just transported from his natural home.

But a factor much more potent is the struggle for existence, and not only a struggle within the race but a struggle outside with a superior race. There is no law in the physical world more relentless than this very struggle for existence and survival of the fittest. From the cradle to the grave it is one continuous fight with man and the elements. It is a struggle for mere living, a struggle for ease and comfort, a struggle against exposure, privation and disease; and in this struggle the weaker die and the stronger live. We may talk of universal brotherhood, but the stronger will rise and rule and the weaker will go to the wall. The denser the population the thicker the fight. It is in the great cities that we see this struggle at its fiercest—the poorer and weaker on one side,

*An interesting example among the lower animals of the fatal influences of a change of habitat is seen in the monkeys brought to this country. They almost invariably die from consumption. I once examined the bodies of a number of monkeys from our menageries and zoölogical gardens, and in every case I found pulmonary tuberculosis in all its stages. The change from the pure air of the forest to the confined and vitiated air of our centres of population is fatal to them.

and the stronger and richer on the other. It is the difference between poverty, hunger and dirt, and ease and comfort and luxury, and a difference greater still, a difference in the sick list and in the death rate; for with poverty and close quarters, with dirt and exposure and crime, come sickness and death. The situation of the colored race is a peculiar one. After being carrled off from their home to a distant land and held in bondage for years, they are suddenly set free and thrown upon their own resources. That they have even in a measure stemmed the tide is indeed to be wondered at. During slavery it must be conceded, I think, that so far as the merely physical man was concerned they were better off. Such bondage would be well physically for a large portion of the white race. They were out of the struggle for existence with their superiors; they were cared for like so many valuable animals; it was to the interests of their owners that they should be; though worked hard, they led regular lives; the dissipations and excesses which enter into the life of a free people they were withheld from; when sick they had the best medical attention obtainable; and all the information which I have been enabled to obtain has satisfied me that the race was a healthy one, even healthier in the main than the white.

But since the war and emancipation things have been reversed. Suddenly thrown upon their own resources their struggle began in the midst of things; freedom gave loose reins to the animal; the doors were opened wide to the vices and excesses of a material civilization; their life became an irregular one; these vices and excesses which like parasites have grown with the growth of our civilization, became a part of their life, and these parasites in their new soil have shot down their roots deeper and have obtained a firmer foothold. This has been the history of the introduction of civilized vices into all uncivilized communities; whiskey, good or bad, certainly disagreed with the poor American Indian, and to-day in India it is playing sad havoc with the multitude. The explanation is that, however small self-control over the appetites exists in the Caucasian it is practically wanting in the savage who drains his cup to the dregs. It is bad enough for the white man but it is worse for his inferior.

Certain writers, like Mr. Tourgée, for example, in their predictions for the future, rely upon "the greater prolificness of the negro," as though the prolificness of any plant or animal were a fixed quantity. But the naturalist knows within what wide limits the prolificness of any plant or animal may vary. That under natural and favorable conditions this prolificness shows a certain rate of increase, and that, on the contrary, when the natural conditions are removed and inimical factors are brought to bear, the rate of increase falls, and may continue to fall to complete extinction. In the study of different organic forms we find of course great differences in the prolificness, depending upon certain laws which have been fairly well worked out.

No one, to my knowledge, has more clearly brought this out, and especially so in its bearings upon the multiplication of the human race, than Herbert Spencer. In his Principles of Biology, Part VI, he treats of the laws of multiplication, an elaboration of a paper which originally appeared in the *Westminster Review* for April, 1852, entitled "A Theory of Population deduced from the General Law of Animal Fertility." Here he points out the antagonism between growth and sexual and asexual genesis, between development and sexual and asexual genesis, between expenditure and genesis, and between nutrition and genesis. He shows us how the vitality of any organic form divides itself between individuation and genesis, between maintaining individual life and increasing the species. He shows us that where these forms are minute and low in the organic scale, with little or no differentiation of parts, and where individuation is almost nothing, the genesis is enormous ; and where, as we rise in the organic scale, there is more individual growth and development, and consequently a greater expenditure of the vitality in this direction, the genesis falls. And further, that inimical factors which in any way reduce the normal quantum of vitality, not only reduce the amount expended upon individuation, but also upon genesis, and the prolificness must consequently fall. We can trace this "moving equilibrium" between individuation and genesis in man as well. Therefore we expect to find in the higher

types of man, with greater differentiation and a more complex brain and nervous system, and where there must necessarily be a greater expenditure towards individuation,—and where genesis itself is more elaborate,—a lower prolificness. And, on the contrary, we find, as we might expect, a higher rate of prolificness among savages than among the Caucasian. But this holds good of the savage only as he is found in his own habitat, and under the natural conditions of which he is the product. Remove him from his natural soil and climate, change his conditions of life and surroundings, and throw him into competition with a superior race, and in a civilization which has been brought about by the growth of that race,—a civilization of which he is not the product,—and he is placed in an abnormal condition, and must suffer physically. And this will show itself in a general deterioration of physique, in a higher rate of mortality, and in a lowered rate of increase.

We see again in certain organic forms a sort of law of compensation where nature seems to provide for great loss of life by a greater prolificness, but these two terms stand to each other as correlatives rather than cause and effect. It is very evident that there can be no such relationship at all comparable in the higher forms of life. Here where inimical factors arise which render individuation more difficult and more precarious, the expenditure of vitality becomes greater in this direction, and so much the greater the more complex is the individuation ; and in like manner the genesis suffers the more, the more complex its processes are. And thus a race which is struggling hard to maintain individual life, and which suffers in addition from an unhealthy living, and from excesses of all kinds, and whose death rate is high as compared with the more favored race, cannot maintain its normal rate of increase, but, on the contrary, must show a diminished prolificness.

And another point worthy of consideration is this : It is not so much a question of How many offspring ? but How many matured and perfected individuals ? In other words, what is the ability to maintain life when started ? And this is what I mean by the vital equation. The figures I have given of

the low rate of infant mortality in Japan are interesting as showing how, in spite of the low birth rate in that country, the low death rate among infants and young children up to the fifth year has led to a large increase in the census returns. And how much better this state of affairs is from an economic standpoint than that of a high rate of genesis with a high infant mortality. How much greater the loss of vitality from the general store of the race! In the first instance there is so much the more vitality to be expended upon individuation, *and that means racial progress;* in the second case, a large amount of the vitality of the race is lost in blighted and immature individuals, and the general level of individuation is lowered, *and that means racial decay.* The laws of propogation have been violated in some way, and the vital equation of the race lowered. And it naturally follows that the more complex the problem of life becomes, the more closely these inimical factors are brought to bear, and the more evident and far-reaching will be the destructive influences upon the race. And here in the United States, which is becoming more and more densely populated with the Caucasian, where the struggle for existence is becoming fiercer, with a great increase in material civilization and all the requirements devolving upon it, all the inimical factors I have enumerated will bear with redoubled force.

And still another point worthy of consideration is this, that despite caste and social barriers, there can be, and is, a physiological fusion of the two races. The extent of this fusion is seen in the mixed element. The exact proportion of this element to the pure negro we are unfortunately unable to indicate, the attempts made by the last census being quite unsatisfactory. This element, I am persuaded, is much greater than is generally believed. I also think that it will increase with much greater strides in the future as the social barriers to miscegenation are removed. As I have attempted to show, this element is largely an unstable one, and of a low vital equation. The process may be likened to a reducing agent, chemically speaking, which borrows vitality from the pure race to produce a new compound which is unstable. The

process may be represented in a different way, again, where the dominant race can be likened to a great polyp which, having surrounded and ingested a smaller community of cells than itself, proceeds to appropriate that which is assimilable, and to throw off that which is foreign and non-assimilable. This great selective process is evident to-day between the two races. Thus thrown into intimate contact they cannot develop on separate lines, each working out its own racial destiny ; there must be a fusion more or less rapid and a struggle for supremacy, where the dominant race holds to its racial traits and its civilization, modified, perhaps, to a certain extent, by what it has appropriated from the inferior race.

I have thus attempted to show that, according to the census, the colored race has not increased at the same rate as the whites, that the colored race is an inferior race, that its physique has deteriorated, and with a consequent higher death rate ; that the mixed element has a lower vital equation, and that all these results are explainable from the teachings of ethnology and biology.

As to the future of the negro in the United States I can see but one goal, and that is defeat, and by defeat I mean an inability to maintain the race as a race with all its characteristics. With the gradual fusion there will be a larger and larger mixed class ; the lighter this element becomes the more the African fades out, and the more the new product approaches the Caucasian. The term "African" will become more and more of a misnomer. Even in the few years, comparatively speaking, which have gone by, the colored population is a quite distinct body from its African ancestors. In this process of fusion and assimilation there will be a great loss of life, but there will long be a Caucasianized element, becoming larger and larger up to a certain point, and I can believe in a vanishing point, so to speak, where it will be hard to trace the alien blood. We see it in many individuals to-day. Its different grades are but as mile-posts on the road to extinction. All this will require time, and probably centuries will go by before the extinction of the race, as a race, will be accomplished.

In the mean time I can see no ground for fear of any great clash between the two races, so much dwelt upon by certain writers. This is a problem which will solve itself. There are more serious social and political problems before us to-day than the poor negro. But of course the care and treatment of this great mass for the present and the near future is a great problem. To most minds the course to be pursued is plain enough, namely, to elevate them, Caucasianize them as far as they will permit it, to treat them as we should treat the lower classes among our own race, educate them, improve their physical condition where we can, in short, make useful citizens of them. How this may be best accomplished involves many questions of government and social science, with which, of course, I have nothing to do.

The whole question but resolves itself into this, that the world has reached a point where the Caucasian is supreme, and all else must give way before him.

SAVANNAH, GEORGIA,
June, 1893.

THE CORRELATION OF STRUCTURE AND HOST-RELATION AMONG THE ENCYRTINÆ.

By LELAND O. HOWARD.

The student of the parasitic Hymenoptera cannot fail to be impressed by the uniformity with which parasites of certain more or less restricted groups are parasitic upon insects of certain groups also of more or less circumscribed extent. Very broad and sweeping generalizations in this direction to which there are, however, many exceptions, may be made. Thus, while the Lepidoptera are parasitized by many representatives of all of the four principal families of parasitic Hymenoptera, those of the subfamily Ichneumoninæ may in general be said to be parasites of Lepidoptera. The species of the braconid subfamily Euphorinæ are, in the main, parasites of Coleoptera, those of the subfamily Microgasterinæ are parasites of Lepidoptera, those of the proctotrypid subfamily Platygasterinæ are parasites of Diptera, mainly of Cecidomyiidæ, and those of the subfamily Dryininæ of the Homoptera of the families Membracidæ, Jassidæ, Tettigoniidæ and their allies. Instances of this kind might be multiplied, but, at the same time, groups in which much less uniformity exists are also numerous.

In the family Chalcididæ, to which the subfamily which I shall particularly discuss belongs, there is the same uniformity in some groups and the same lack of uniformity in others. Very few of the subfamilies may be said to possess any great uniformity throughout their whole extent. The Tetrastichinæ, however, appear to be uniformly parasites of other parasitic Hymenoptera, while the Elachistinæ are parasites (mainly external) of Lepidoptera, and the Toryminæ are parasites of gall-insects, the preference of the latter depending not so much upon the structure of the host as upon its possession of the gall-making habit, since they attack cynipid, cecidomyiid, trypetid, and even lepidopterous gall-makers.

In the majority of the subfamilies, however, there is a much greater subdivision of the correlation of structure and habit, frequently descending to genera, and often apparently to species.

A lengthy series of interesting though occasionally apparently conflicting facts could be gained by the careful study of the host-relations of the species of any one of these subfamilies, but in undertaking such a study it is prerequisite that the group shall have been well classified from morphological details and that very extensive rearings shall have been made. These two prerequisites debar us at the present time from any but initial attempts at generalizations with most of the groups where the general trend of habit is not at once evident. It is even too soon to secure the best view of the conditions in the subfamily which I have chosen, but sufficient facts are available to render study and arrangement of interest and perhaps of importance.

The Encyrtinæ of Europe have been carefully monographed by that learned and able entomologist, Dr. G. Mayr, of Vienna, (Verh. d. K. K. Zool-Bot. Ges. Wien, 1876). Nearly all of the European forms have passed beneath his analytical eye and a model systematic paper has resulted. He has also collated and displayed in an instructive table all biologic facts known concerning the species of that fauna.

Originally drawn to the study of the group through its economic importance as containing so many parasites of injurious Coccidæ, the writer has, at unfortunately rare intervals, since 1880 studied the structure of the North American forms with the unrivalled advantages offered by the collection of the U. S. National Museum. The European species accepted by Mayr in 1876 numbered 102, distributed in 25 genera. The North American species contained in the National Museum, number about 150. Twenty of the 25 European genera have been found to have representatives in our fauna while representatives of 14 new genera have been found. The 150 species of the Museum collection have all been carefully studied generically and have been generically placed, although only about 50 have received specific description and name. This is our

basis for the first of the prerequisites—that of systematic classification from structure alone.

For the second, knowledge of host-relations, we have Mayr's table and the extensive rearings and notes of the Division of Entomology of the U. S. Department of Agriculture, which my chief, Dr. C. V. Riley, permits me to use for this purpose, as well as his own personal notes made mainly in Missouri prior to 1876. In all these comprise more than 200 rearings and of the 150 species in the National Museum collection, about 120 have been reared and the host-insect identified with sufficient accuracy for our present purpose.

Let us see then how far uniformity of habit goes in this group, by taking up one after another of the described genera :

Rhopus Förster.—*European :*—Coccus racemosus.
American :—Pseudococcus aceris, (Ill.) Dactylopius ephedræ (Cal.)

Holcothorax Mayr.—*European :*—Lithocolletis 5 spp., Tischeria complanella, Nepticula splendidissimella, Hyponomeuta 4 spp., Plusia moneta.

Aphycus Mayr.—*European :*—Coccidæ 9 spp., nearly all Lecaniinæ.
American :—Lecanium, 9 spp., (Mo., S. C., Ala., Cal., Va., Oreg. Fla.) Dactylopius, 2 spp., (Cal.) Ceroplastes, 2 spp., (Ariz., N. Mex.) Kermes 1 sp., Pulvinaria innumerabilis, (Ia.) Diaspis rosæ, (N. J.) Mytilaspis citricola, (Fla.)

Blastothrix Mayr.—*European :*—Coccidæ, 9 spp., mainly Lecaniinæ.
American :—Lecanium, 4 spp., (N. Y., Cal., Fla.), Pseudococcus yuccæ (Cal.)

Psilophrys Mayr.—*European :*—Lecanium sp.

Leptomastix Fœrst.—*American :*—Dactylopius destructor, (D. C.)

Copidosoma Ratz.—*European :*—Agrotis fumosa, Hadena polyodon, Leucania albipicta, Plusia 5 spp., Catocala electa, Geometra, Cidaria variata, Eupithecia 4 spp., Tortrix sp., Carpocapsa splendora, Hyponomeuta 2 spp., Cerostoma sp., Depressaria 2 spp., Gelechia favilaticella, Lita alsinella, Tachyptilia populella, Coleophora, 2 spp.
American :—Papilio turnus, (W. Va.) Celæna renigera, Plusia brassicæ, (many states.) Aletia xylina, (Ark.) Acronycta sp., (Mo.) Unknown Noctuid larvæ, 3 spp., (Colo., Ont., Quebec.) Sericoris coruscana, (N. H.) Gelechia gallæsolidaginis, (Mo.) G. pseudacaciella, (D. C.) G. gallæasterella, (N. J.) G. sp. (Ala.) G. viburnella, (Mo.) G. epigæella, (Va.) Tinea granella, (D. C.) Bucculatrix thuiella, (Mo.) Coleophora sp., (D. C.) Lithocolletis fitchella, (D. C.) Unknown Tineid larva, (Mo.)

Bothriothorax Ratz.—*European :*—Syrphus larva, Anthomyia cepa-rum.

American :—Syrphid larva, (Va.) Syrphid larva feeding on Rose Aphis, (Cal.) About to oviposit on Syrphid larva, (N. Y.)

Chiloneurus Westw.—*European :*—Coccidæ, 4 spp., probably all Le-caniinæ.

American :—Lecanium spp., (Ia., Va., D. C,, Wis,, Mo.) Dactylopi-us destructor, (D. C.) Dactylopius sp., (Cal.) Kermes sp., (Tex.) Diaspis rosæ, (Cal.) Aspidiotus sp., (Cal.)

Comys Först.—*European :*—Coccidæ, 10 spp., apparently all Lecaniinæ.

American :—Lecanium, 5 spp., (D. C., Ala., La., Cal.) Pulvinaria sp., (no locality.) Kermes sp., (N. Y.)

Homalotylus Mayr.—*European :*—Coccinellid larva, Galeruca calmari-ensis.

American :—Cycloneda sanguinea, (Fla.) Unknown Coccinellid lar-væ, (Fla., Ia., N. Y., N. Mex.) Anatis 15-punctata, (Mo.)

Cerchysius Westw.—*American :*—Icerya rosæ, (Jamaica, B. W. I.)

Isodromus Howard.—*American :*—Chrysopa cocoons, (Cal., N. C., Mo., D. C., Tex., Fla., N. Mex.)

Pentacnemus Howard.—*American :*—Bucculatrix thuiella, (Mo.)

Tanaostigma Howard.—*American :*—Larva of Tychea, (Cal.)

Rileya Howard.—*American :*—Dactylopius, (Cal.)

Cerapterocerus Westw.—*European :*—Coccidæ, 5 spp.

Habrolepis Fœrst.—*European :*—Coccidæ, 4 spp.

Phænodiscus Fœrst.—*European :*—Coccidæ, 6 spp.

Ericydnus Walk.—*European :*—Lecanium vitis.

Bæocharis Mayr.—*European :*—Undetermined Coccid.

Dinocarsis Fœrst.—*American:*—Thyridopteryx ephemeræformis, (Fla.)

Encyrtus Dalm.—*European :*—Eumenes coarctata, Ceuthorrhynchus assimilis, eggs of Bombyx neustria, eggs of Lasiocampa pini, eggs of Notodonta, unknown Lepidopterous eggs, larva of Eupithecia 2 spp., Syrphus larva, Cecidomyiid galls, 2 spp., Aphis sp., Coccidæ, 15 spp.

American :—Cynipid gall on Oak, (Ala.) Nest of Ceratina dupla, (N. Y.) Ichneumonized cocoon of Artace punctistriga, (Fla.) Eggs of Buprestid, (Cal.) Eggs of Clisiocampa sp., (?) Larva of Desmia maculalis, (Mo.) Eupithecia miserulata, (Me.) Bucculatrix pomi-foliella, (N. Y.) Bucculatrix sp., (D. C.) Laverna sp., (Mo.) Mesograpta polita, (Fla.) Cecidomyia s.-siliqua, (N. H.) C. s.-batatas, (Mo.) Eggs Anasa tristis, (Fla.) Eggs Prionidus cristatus, (Tex.) Heteropterous eggs on Pine, (Cal.) Trioza diospyros, (Fla.) T. magnoliæ, (Fla.) Pachypsylla celtidis-gemma, (Mass.) Psyllid on Arbutus, (Cal.) Psyllid on Amelanchier, (D. C.) Aphis brassicæ, (Fla.) Megoura solani, (Fla.) Glyphina eragrostidis, (Ind.)

Pemphigus spirothecæ, (?) Siphonophora avenæ, (Ind.) Aphis pruni, (Ia.) Lecanium, 3 spp., (Cal., Fla., Mo., Neb.) Pulvinaria innumerabilis, (Mo.) Dactylopius destructor, (Fla.) Kermes, 3 spp., (Cal., N. Y., Mo.) Aspidiotus corticalis, (Fla.) Diaspis roæ, (D. C., Mo., Cal.)

From this condensed statement certain interesting facts plainly appear. Rhopus, Holcothorax, Aphycus, Blastothrix, Psilophrys, Leptomastix, Chiloneurus, Comys, Cerchysius, Rileya, Cerapterocerus, Habrolepis, Phænodiscus, Ericydnus and Bæocharis, or 15 out of the 23 genera of which we know the habits, are parasitic upon bark lice exclusively. Copidosoma, Pentacnemus and Dinocarsis are parasitic exclusively upon lepidopterous larvæ. Bothriothorax is parasitic upon dipterous larvæ only. Homalotylus is parasitic exclusively upon coleopterous larvæ of the families Coccinellidæ and Chrysomelidæ. Isodromus is parasitic exclusively upon Chrysopa larvæ, issuing from their cocoons. Tanaostigma is parasitic upon the larvæ of seed-inhabiting weevils.

Thus far there has been absolute uniformity in host relation within generic bounds in so far that the host insects of each particular genus are closely related and of the same general type. There is one genus remaining, however, which is a biological complex and, from the uniformity which has existed among other members of the group, the natural inference that it is also a morphological complex would be justified. Close study of the classificatory characters bears out this assertion. Encyrtus is one of those unwieldy genera of varying limit, found in nearly every large family of insects, in which many species have been lumped, frequently for insufficient reasons, and really for want of a better place to put them. Up to a certain stage in the classification of the group, authors have not felt justified in separating the species generically, since their characters have not seemed as important as those which have been considered of generic value, while the subgenus is an element of convenience or confusion, according as you may view it, which has not as yet been adopted to any extent in entomology. Encyrtus is such a genus. Coming at the end of a synoptic table, by a process of elimination the refuse has

been left for this unfortunate group. Its definition lacks that trenchant clearness characteristic of Mayr's other generic characterizations, and what are really diverse types to-day bear this generic name.

In glancing through the host insects which species of Encyrtus affect we find in Europe a wasp larva, a beetle larva, the eggs of noctuid and bombycid moths, the larva of a micro-lepidopter, the larva of a syrphus fly, dipterous galls, plant lice and bark lice. We have thus 8 types of host insects. In America we have also a wasp larva as well as two other hymenopterous hosts, viz. : an Ichneumon and a cynipid gall. We have also the eggs of a bombycid moth and of a beetle, the larva of a micro-lepidopter, larva of a syrphus fly, dipterous gall-makers, plant lice and bark lice, and two new elements in addition to the beetle eggs and the hymenopterous insects mentioned above, viz., heteropterous eggs and Psyllidæ. We have then 12 quite distinct types of hosts, all told, 8 of them occurring in Europe and all in America.* With this view of the biology of the genus it at once becomes important to make a closer study of the morphological aspect of the individual forms than has yet been done. One would naturally expect to find an assemblage of characters grouping together those species which prey upon a common type of host, and, such characters being found, shall we not be justified in giving them greater classificatory weight than parallel separating characters which are not correlated with important, not to say vital, biologic facts?

No attempt has hitherto been made in this direction. To test provisionally the aptness of the idea, a brief survey of the synoptic table of European species shows that while no attempt has been professedly made to form natural groups, yet the characters hit upon to conveniently analyse the species have brought into immediate juxtaposition the species parasitic upon lepidopterous eggs; those parasitic upon dipterous larvæ are brought into close connection; the bark-louse para-

*Should the species of Encyrtus described by Girard as coming from a Psyllid gall prove to belong to this genus, Europe will have representatives of 9 of the types.

sites are lumped, and those parasitic upon lepidopterous larvæ occur together, although separated widely from those parasitic upon the eggs of the same order.

And now as to the results of an examination of our American forms:

It will not be necessary in this paper to go into detail as to the structural peculiarities which have been found upon this examination. They will be summarized elsewhere in connection with the descriptions of the new genera necessitated by this investigation. The conclusions arrived at, however, are as follows:

Among the species parasitic upon Coccidæ we find three distinct types two of which will form new genera. The most abundant is parasitic upon Lecaniinæ and Coccinæ, the second upon Diaspinæ while a third and isolated type is reared from a lecaniine—Pulvinaria innumerabilis.

The species parasitic upon Aphididæ possess a common facies and form an independent type in the group distinguished by well-marked structural characters.

Among those parasitic upon Psyllidæ we find an interesting state of affairs. Those reared from gall-making Psyllidæ belong to the same type as that reared from a gall-making cecidomyiid, while those parasitic upon nearly free-living Psyllidæ belong to two types, distinct from each other and from the first, and dividing upon geographical lines, the one being east coast and the other west coast.

The parasites of the free-living dipterous larvæ belong to a common type distinct from the others, while that reared from the dipterous gall-maker agrees in facies and in main structural characters with those just mentioned from psyllid galls.

The species reared from a cynipid gall, however, forms still another type and the most distinctly marked one of the whole series.

The species reared from lepidopterous larvæ belong to a common type, distinct from the rest, but most closely resembling the forms reared from free-living dipterous larvæ.

Those reared from heteropterous eggs and those from lepidopterous eggs belong to a common type and while separable

from each other by certain structural characters, these seem unimportant compared with those which we have been using, and for the present, at least, these parasites must remain congeneric.

The single species reared from a beetle egg forms an isolated type in the group as does also the single species reared from an ichneumon cocoon.

That reared from Ceratina is a single specimen lacking antennæ and these organs furnish the principal characters of the European E. varicornis which we should expect it to resemble from the fact that the latter was reared from Eumenes. The other structural characters given are not especially distinctive, but it is worthy of note that they agree with those of our Ceratina parasite.

We have then, in summing up, fourteen distinct types of the genus Encyrtus to the discovery and exact definition of which we have been led by a knowledge of the host-relations of the species. Upon thirteen of these types new genera will be founded, leaving to the fourteenth the old generic name. Those parasitic upon Aphididæ, Cynipidæ, lepidopterous larvæ, coleopterous eggs, ichneumonid cocoon and bee larva form each a distinct type. Those parasitic upon Coccidæ form three, two of which are well differentiated biologically by the character of the host-insects within the family. Those parasitic upon Psyllidæ and Diptera form three and two respectively, one of which is possessed by both in common, the gall-making habit of the host producing the similarity in the parasite, as is common in other parasitic groups. And these parasitic upon heteropterous and lepidopterous eggs form a single type, as is also occasionally the case with other parasitic groups.

This little paper then tends to show: (1) Another exemplification of the axiom that structure is dependent upon habit; (2) that while the true classification depends entirely upon structural detail, we may gain ideas as to the relative value of characters by a knowledge of vital habits; and (3) that as soon as sufficient records accumulate it will be important to examine the classificatory bearings of the group-habits, par-

ticularly of the host-relations, with other groups of parasitic Hymenoptera.

I am perfectly aware that after all I have touched only upon one side of this important subject. The other side is the structural differentiation of forms whose host-relations are identical. Parasites of several genera and even families are parasitic upon the same host-type and even upon the same individual. Comparatively widely different factors must here influence the structure and a wide field of investigation is thus opened.

WASHINGTON, D. C.,
August 9, 1893.

THE FERMENTATION TUBE WITH SPECIAL REFERENCE TO ANAEROBIOSIS AND GAS PRODUCTION AMONG BACTERIA.

By THEOBALD SMITH.

In the study of the microscopic forms known as bacteria we have what might be fitly called the focal point of the various branches of biological science. Though their investigation may require careful morphological researches yet the unmistakable monotony of form, combined with a considerable variation of physiological activity, has compelled the bacteriologist to pay much attention to means by which such physiological variations may be more or less accurately registered in order that they may serve as a supplementary basis for classification. Again, with unicellular organisms the manifestations of cell activity become the most important phenomena for study. These manifestations bring together the fields of physiology and chemistry and make bacteriology in one sense a branch of physiological chemistry.

In dealing with bacteria and the results of their activity, one fact strongly impresses us and that is the necessity of knowing precisely and unmistakably the organism before us. No matter how profound the physiological and chemical studies of bacterial life, unless they are linked to an organism readily identifiable they have failed to assert their full value. In all the investigations of bacteria in their relation to the fermentation industries, to the dairy, to the soil, and to human and animal diseases now going on, the element of fundamental importance is the organism itself. About this all functions are grouped, to this every question finally reverts. The necessity for more accurate means of recognizing species and varieties has, however, not generally been felt and the methods of diagnosis have not kept pace with progress in the more practical

fields of microbiology. The species studied some years ago are assuming a more and more hazy outline and questions are constantly arising concerning the possible identity of old with new forms. This condition is largely unavoidable in a young and rapidly growing department of science and is in part due to the fact that investigators are too prone to attack new problems before the more orderly work concerning the old ones has been completed. For this state of affairs they are hardly to be blamed, for the profound relations of bacteria to other life on our globe has given the study of them a practical bias without which the resources now employed in investigations could never have been wrested from the utilitarianism of our present social organization.

It is due to considerations such as these that this article is presented as a contribution to the methods by which bacteria may be more definitely recognized. A complete differentiation is possible only through a complete knowledge of the biology of any given organism. This knowledge is only gradually acquired and more or less temporary expedients must be resorted to to fix the hosts of microörganisms shading into one another by almost intangible gradations of form and function. Among these expedients the fermentation tube occupies an important place in the differentiation of the more saprophytic forms and in giving us a fairly good conception of their powers of fermentation. I can do no better therefore in commemoration of the present occasion than to offer the observations which I have made with it during the past four years, as a connected whole to the biologist.

The fermentation tube appears to be an apparatus of considerable antiquity. The bent tube closed at one end has been used by chemists in storing small quantities of gas for qualitative analysis. I have been unable to determine who was the first to apply it to fermentation processes. In Detmer's *pflanzenphysiologisches Practicum* I find it figured as *Kühne'sches Gährungsgefäss.* More recently it has been adapted by Einhorn[1] for the quantitative determination of sugar in urine and by Doremus for the quantitative determination of urea in the same fluid. In 1889 I conceived the idea of using this tube as an ordinary culture tube in order to determine something more definite concerning the production of gases by bacteria without resorting to the complex manipulations of the chemist[2]. The form of the tube used in the following study

is given half size in the plate (fig. 1). It is essentially a tube bent at an acute angle, closed at one end and enlarged at the other into a bulb. At the angle the tube is more or less constricted. To it a glass foot is attached so that the tube may stand upright. For the sake of uniformity, the closed portion of the tube will be denominated "closed branch," the open portion, "the bulb," the intermediate narrow, bent portion the "connecting tube."

In the construction of this simple bit of apparatus several points must be borne in mind. The bulb should be large enough to receive all the fluid contained in the closed branch, for in some kinds of fermentation, the gas production drives out all the fluid from the closed branch. The cotton-wool plug must not be moistened under such circumstances otherwise the purity of the culture is imperilled. If the bulb is sufficiently large this difficulty will not arise. The connecting tube should not be too small, for then the filling and emptying of the closed branch becomes very tedious. Nor should it be too large, otherwise the anaërobic properties of the fluid in the closed branch, to be discussed farther on, may be less effective. Lastly the angle formed by the two branches of the tube must not be too acute otherwise the tube must be tilted so much during the transferrence of the fluid from the bulb to the closed branch that there is danger of its moistening the plug or even running out of the bulb. Since the closed branch is not accessible to cleansing with a brush it is advisable to fill the tube after use with the ordinary cleaning mixture (bichromate of potash and sulphuric acid) and allow it to stand undisturbed for some days.

The filling of the tube with culture fluid does not give rise to any difficulty. The fluid is poured into the bulb until this is about half full. The tube is then tilted until the closed branch is nearly horizontal so that the air may bubble up through the connecting tube and permit the fluid to enter the closed branch. When this has been completely filled, enough fluid should be added to cover the lowest expanding portion of the bulb. If the tubes are likely to remain unused for a month or longer it is best to add fluid until the bulb is half full to allow for evaporation.

The sterilization requires a few suggestions. This is best done in a steamer like the 'Arnold' for the tubes can be placed directly on the perforated plate in the bottom of the steam chamber. If a steamer is not at hand, an ordinary tin or granite-ware pail having a tight cover may be used. Enough water is poured in to form a shallow layer. To prevent the upsetting of the tubes by the ebullition I have been in the habit of placing them, three or four together, into perforated cups which are placed directly on the bottom of the pail. Steaming or boiling on three consecutive days is sufficient for complete sterilization. During the boiling the tension of the aqueous vapor in the closed branch

forces much of the fiuid into the bulb. As soon as the lid is removed the fluid returns to its former place in the closed branch with the exception of a small space at the top which is occupied by air originally dissolved in the liquid and driven out by the boiling. This air bubble should be tilted ont. After the second boiling some air may still be present. If this be tilted out the fluid will be fouud entirely free from air after the third or last boiling.

PHENOMENA OF ANAEROBIOSIS AND REDUCTION.

For the cultivation of bacteria the fermentation tube consists of two quite distinct portions sharply demarcated at the place indicated by the line *xy* in fig. 1. The bulb contains fluid in direct communication with the air while the fluid in the closed branch is almost entirely shut off from any such communication. Moreover, during the process of sterilization, the fluid in the latter has been entirely freed of air, as described above. This oxygen-free condition of the fluid is very clearly demonstrated by the following simple experiment:

If to peptone bouillon be added a few drops of a concentrated aqueous solution of litmus, methylene blue or indigo-carmine, and fermentation tubes be filled with this colored fluid and sterilized, the fluid will be decolorized during the boiling by reducing processes due to the organic substances in the peptone bouillon*. In the open bulb the presence of air very speedily causes a return of the color. In fact it may not completely disappear at any time. If the tubes containing the colorless, reduced litmus or methylene blue be allowed to stand in a place sheltered from sudden changes of temperature, the fluid in the closed branch remains free from color (with perhaps a faint indication of color near the connecting tube) until the time arrives when the fluid in the bulb has evaporated and a bubble of air escapes into the closed branch.†

* I at first conceived the reducing action due to the glucose only, but the same process went on in peptone bouillon free from glucose. It is not due to simple boiling, however, for litmus or other coloring matter contained in simple bouillon or in water with or without a little Na_2CO_3 remains unchanged in the sterilization. It is thus dependent on the presence of glucose or peptone.

† This occurrence is like the escape of air into the reservoir of a student lamp which brings about the continuous feeding of the wick with oil.

Then the color begins to return and shows itself first at the very top of the closed branch beneath the air bubble. Thence it spreads slowly through the liquid as the evaporation continues to bring more air into the closed branch. These facts make it clear why the connecting tube should be as narrow as is compatible with the ready filling and emptying of the closed branch, for the smaller the calibre of this tube the less the interchange of fluid between open and closed portion.

Let us now consider the effect which this oxygen-free state of the culture fluid has upon the multiplication of bacteria. There is first of all a class of bacteria which multiply remarkably well in the bulb and the connecting tube but the fluid of the closed branch is shunned by them so thoroughly that it remains perfectly clear and limpid. The line of demarcation between the turbid, teeming liquid of the bulb and connecting tube, and that of the closed branch is sharply drawn. Evidently this class of bacteria are not only unable to multiply in fluids deprived of oxygen but they seem to avoid them as if influenced by a negative chemotaxis in spite of the power of motion which many of these forms possess. This limitation of growth has been observed in case of the same species from widely different sources as to time and place and hence stands for a constant character of the species. To this class belong many spore-bearing bacilli found in nature (*Bacillus subtilis*) and other forms (*Bacillus fluorescens liquefaciens*), and it corresponds to the class long known as the obligatory aërobic bacteria. The old test for this class, introduced by R. Koch, was an incapacity to multiply under a mica plate laid upon the gelatine layer in which the bacteria were supposed to be multiplying.

A second group of bacteria multiply not only in the open bulb but also in the closed branch. The fluid becomes uniformly clouded but the growth soon subsides for there is in most cases a decided preference for the open bulb, varying slightly with different species. In this the density of the growth always corresponds to that of cultures in ordinary cotton-plugged test tubes containing the same fluid. To this

class belong the greater number of the gas-producing bacteria to be considered farther on. It corresponds to the facultative anaërobic group, that is, those forms which are capable of multiplying to a certain extent in media free from oxygen although they flourish best in the presence of this gas.

There is lastly a third group of bacteria, of which I have examined only a small number in the course of the past four or five years, which do not multiply in the open bulb but seek the closed branch. These are the strictly anaërobic forms which require a medium devoid of oxygen. Many of them are gas-producing.

The fermentation tube thus informs us at once to which of these three groups of bacteria any given species belongs. This determination is especially valuable with the facultative anaërobic and the aërobic species. The anaërobic nature of any given form is usually manifested beforehand by its refusal to multiply in the ordinary culture tubes. It is needless for me to go over the various methods and devices which have been and are still employed in defining the aërobic or anaërobic character of bacteria. They are given in part in current text books. The simplicity of the test in the fermentation tube will at once appeal to all who have striven to produce a vacuum or substitute for the air an atmosphere of hydrogen.

The possibility of cultivating aërobic and anaërobic bacteria in the same kind of tube makes more simple certain bacteriological work carried on hitherto under considerable difficulty and with but partial success. In the determination, both quantitative and qualitative, of bacteria in the soil or the intestinal tract for instance, the aërobes and anaërobes had to be dealt with separately. In the solution of such problems the fermentation tube may do good service if the method of dilution be employed. Since this tube shows no discrimination between these two physiological groups of bacteria all would have an opportunity to develop. I am well aware of the difficulties inherent in the method of dilution,—the difficulty of gauging the dilution beforehand, the large number of tubes required, the care to be taken in the manipulation of the fermentation tubes, their size and cost—but these diffi-

culties are not those which threaten the success of the work and they count for little in important special investigations.

The Reducing Action of Bacteria.—It has been known for some years that certain bacteria have the power of abstracting oxygen from compounds which hold it very loosely. It has been customary among bacteriologists to demonstrate this deoxidizing or reducing activity by adding certain substances to the culture fluid which are colored in the oxidized state but which lose their color in the reduced state. Among the substances used are those mentioned above in the discussion of the anaërobic properties of the tube, and the action of bacteria correspond precisely to the action of heat in the presence of glucose or peptone as has been already described. It is not my intention to discuss this interesting phenomenon of reduction among bacteria excepting to call attention to the fermentation tube in bringing it out.

It will be remembered that when methylene blue, or indigo carmine or litmus be added to peptone bouillon with or without glucose so that the fluid becomes distinctly colored, and the tubes steamed, the fluid in the closed branch becomes decolorized. If bubbles of air be tilted into the closed branch and out again repeatedly, the color returns. Such tubes inoculated with any bacteria which are capable of growing in the closed branch, if only to a slight degree, become within 24 hours completely decolorized, with the exception of a shallow layer of fluid in the bulb. In the closed branch, for reasons already given, the fluid remains indefinitely decolorized. In the bulb the color returns when for any cause the growth ceases and subsides. It is interestiug to note that in an ordinary bouillon culture of *B. coli*, the phenomena of reduction and oxidation could be witnessed for 15 days at the end of which period the culture was rejected. The methylene blue would lose its color within half an hour after it had been re-oxidized by allowing air to bubble up into the closed branch. If a small quantity of air was allowed to remain in the closed branch, a stratum of blue fluid would remain at the top of the fluid column near the air for some days, then disappear completely, thereby indicating the complete consump-

tion of the oxygen admitted to the confined space, by the vital activity of the bacteria. Again in glucose bouillon inoculated with hog cholera bacilli, the complete paralysis of the bacteria after a certain stage in the fermentation is very clearly demonstrated by a permanent return of the color of the fluid in the bulb. The contrast between the deep blue color in the latter and the yellowish hue of the decolorized fluid of the closed branch is very striking.

THE PRODUCTION OF GAS BY BACTERIA.

Attention has been called to the formation of gas by bacteria by a number of writers in the past. Thus Escherich[3] in 1885 demonstrated the fact that *B. coli* and *B. lactis aërogenes*, both bacteria of the intestinal tract described by him for the first time, produce gas in solutions of glucose and lactose. In 1886, Arloing[4] called attention to the same subject. The property of gas production had been long associated with the pathogenic bacillus of "black quarter" in cattle (*Rauschbrand, charbon symptomatique*) which produces gas in the tissues of the affected part. Similarly the anaërobic bacilli of tetanus and of malignant œdema are known as gas producers. Among these anaërobes the formation of gas was demonstrated by distributing the bacteria in deep layers of liquid agar containing glucose and congealing the agar at once. The formation of numerous gas bubbles throughout the agar and the breaking up of the jelly by large quantities of gas is described and pictured and is now a common sight in bacteriological laboratories. A large number of bacteria belonging mainly to the group of facultative anaërobes, are now known as gas producers. Nevertheless the production of gas by bacteria has not thus far been taken as a serious matter by bacteriologists in the differentiation and fixation of species and varieties. Many have of late years been in the habit of recording the presence or absence of gas in cultures, but by methods likely to mislead. Since the gas test has proved the only final means of differentiating two important species, *B. coli communis* and *B. typhosus*, much more attention has been paid to this function but the methods have not materially improved.

In spite of the fact that I called attention to this matter three years ago[1] by describing a procedure for determining the production of gas as simple as the ordinary cultivation of bacteria, this procedure has not been generally adopted largely because the fermentation tube itself seems to be looked upon as something beyond the range of the ordinary bacteriological outfit.

In referring to gas formation writers have been in the habit of calling attention to the gas bubbles which make their appearance under certain conditions in stick (*Stich-*) cultures in gelatin and agar as well as in inclined or "slant" cultures of agar if there is condensation water present. These bubbles appear in the depths of the gelatin, one or more days after inoculation, as flat, lenticular spaces cleaving the jelly in one or more directions. In agar stick cultures, kept at 37° C. they appear frequently within 24 hours after inoculation within the depths of the agar jelly. In slant cultures they are usually found between the agar and the sides of the tube, imprisoned there by the condensation water which fills the gap between the slightly retracted agar and the glass. These bubbles depend for their presence on two things: 1, The capacity of the particular species for fermenting glucose with the production of gas; and, 2, The presence of glucose in the meat used in the preparation of the nutrient gelatin or agar. As I shall point out farther on the meat infusion is in some cases entirely free from such fermenting substance and if accidently used the bubbles will not appear. This test is therefore unreliable. A much better method and one which should not be neglected if the fermentation tube is not at hand is to add a definite quantity of glucose (or some other carbohydrate) to the gelatin or agar. Gas bubbles will invariably appear if the species is capable of producing gas at all. So far as my observations have gone they show that all gas production is linked to the presence of glucose or some other carbohydrate in the culture medium. Before giving illustrations of this process among different bacteria a few remarks on the manipulation of the fermentation tube are in order.

The fluid used in all cases, with exceptions to be mentioned, was peptone bouillon containing either glucose, lactose or

saccharose. The bouillon was prepared by digesting fresh beef in water at 60° C. for several hours then filtering and adding ¼ per cent. peptone, ½ per cent. sodium chloride and about 3cc. of a normal solution of sodium carbonate for every hundred cc. of the fluid. This suffices to make it feebly alkaline. To this peptone bouillon 2 per cent. of one or the other of the three sugars mentioned was added and the resulting fluid sterilized in the fermentation tubes.

These are kept, after inoculation, in the thermostat at 37° C. A mark made on the sides of the closed branch at the end of every 24 hours with a glass pencil furnishes an approximate record of the rate of gas production. Unless this is done it is impossible to know precisely when the formation of gas is at an end and also whether or not the volume of gas has been diminished by absorption. It is best to wait 4 or 5 days after the production has ceased before making a final examination. This is done by noting the condition of the growth, the reaction of the fluid in the bulb* and the maximum quantity of gas produced. This is most easily done by laying directly on the tube a glass millimeter rule and noting the tube length occupied by gas. The entire length of the closed branch is also noted, making due allowance for the upper convex extremity and the lower constriction. This mode of measurement is sufficient since only comparative values are desired. For the same reason all barometic and thermometric corrections are omitted in these approximate estimations.

The examination of the gas produced was limited to the determination of the quantity of carbon dioxide and of the explosive character of the gas remaining after the absorption of CO_2 by sodium hydrate. These facts are determined by the following simple manipulations:

The bulb is completely filled with a 2 per cent. solution of NaHO and closed tightly with the thumb. The fluid is shaken thoroughly with the gas and allowed to flow back and forth, from bulb to closed branch and the reverse several times

*The reaction was noted by placing a drop of the fluid on delicate litmus paper. The cultures were occasionally boiled to drive off any CO_2. In no case did the reaction with the litmus paper change.

to insure intimate contact of the CO_2 with the alkali. Lastly, *before removing the thumb, all the gas is allowed to collect in the closed branch* so that none may escape when the thumb is removed. If CO_2 was present, a partial vacuum in the closed branch causes the fluid to rise suddenly when the thumb is removed. After allowing the layer of foam to subside somewhat, the glass scale is again applied to the closed branch and the amount of CO_2 absorbed may thus be measured. In all cultures of this character thus far examined the gas remaining was explosive in character and probably hydrogen. At any rate wherever hydrogen is referred to hereafter, it simply signifies an explosive gas whose analysis must be left to the chemist. The explosive character of this residue is easily demonstrated as follows :—The cotton plug is replaced and the gas in the closed branch allowed to flow into the bulb and mix with the air there present. The plug is then removed and a lighted match inserted into the mouth of the bulb. The intensity of the explosion varies with the quantity of air present in the bulb.

One difficulty with the culture fluid employed needs to be mentioned at the outset. It is the presence of a small, but variable amount of glucose in the beef or other meat employed. When only glucose is used the difficulty disappears, but when other sugars are used we are at a loss to know how much of the gas to ascribe to the glucose originally present in the beef infusion or even to know whether the other sugars added are at all attacked by the bacteria. Recently I tested beef broth as it was prepared from time to time in the laboratory by inoculating fermentation tubes filled with it with a variety of gas-producing bacteria. In the following table the total amount of gas is calculated in percentages of the total volume of the closed branch which is about 20 ccm. The amount of CO_2 absorbed by potash is given in percentages of the total volume of gas. The gas remaining is explosive.

I.—Total Gas Set Free in Meat Broths, etc., by Various Gas-Producing Bacteria.

Culture Fluid.	*B. cloacæ.*	*B. lactis ærogenes.*	*B. coli.*	*B. choleræ suis.*	*Proteus vulgaris.*
Peptone bouillon (beef) A	. . . . .	33 pr ct. (CO_2=30 pr ct.)	27 pr ct.* (CO_2=33 pr ct.)	. . . . .	. . . . .
" " " B	14 pr ct. (CO_2=11 pr ct.)	. . . . .	. . . . .	10 pr ct.	1 pr ct.
" " " C	22 (CO_2=15)	. . . . .	15 (CO_2=22)	. . . . .	2.5
" " " D	0	0	. . . . .	0	. . . . .
" " " E	27 (CO_2=16)	. . . . .	. . . . .	. . . . .	. . . . .
" " " F	22, 23, 24 (CO_2=17)	. . . . .	. . . . .	. . . . .	. . . . .
" " " G	19	10	. . . . .	. . . . .	. . . . .
" " " H	12	. . . . .	. . . . .	4	. . . . .
" " " I	0	0	. . . . .	. . . . .	. . . . .
" " " J	. . . . .	. . . . .	22 (CO_2=37)	. . . . .	. . . . .
" " (veal)	26	. . . . .	. . . . .	. . . . .	. . . . .
Bouillon (pork)	2	. . . . .	. . . . .	. . . . .	. . . . .
Dunham's solution	. . . . .	0	0	0	. . . . .

* See fig. 8 of Plate.

This table shows that of ten samples of beef broth two were manifestly free from glucose. Hence the advice of Dunbar[5] to use simply beef infusion (*Fleischwasser*) to test the gas producing power of bacteria would lead to conflicting results unless glucose were added. That the sugar contained in muscular tissue is glucose as affirmed by physiologists seems to be borne out by the fact that it is attacked by bacteria which do not ferment lactose or saccharose.

In order to eliminate the source of error introduced by the muscle sugar I tried a solution of salts reccommended by Fermi[6] and of the following composition:

$MgSO_4$	0.2	gram.
HK_2PO_4	1.	"
$(NH_4)_3PO_4$	10	"
Glycerin	45	"
Water	1000	cc.

In this solution the bacteria experimented with failed to multiply when peptone was added and the glycerin omitted. When both were present the fluid in the open bulb became fairly turbid but that in the closed branch remained practically free from any growth. Evidently the glycerin could serve as food only in presence of oxygen. When glucose was added gas appeared, but much more slowly and in much smaller quantity than in peptone bouillon with glucose. A comparison of results obtained with this artificial solution and peptone bouillon was not possible and further trials with it were abandoned.

It next occurred to me that the sugar in bouillon might be removed by allowing some gas-producing bacteria to multiply in the latter for a time. The bouillon might then be resterilized after a certain quantity of some sugar had been added and the fluid reinocculated with the species to be studied. This procedure was found successful so far as gas production is concerned, but it went on more slowly and apparently in a somewhat different way. Hence this method was given up.

Dunham's solution (1 per cent. peptone and ½ per cent.

sodium chloride in water) was also tried. Bacteria multiplied so feebly in it, however, that it also was abandoned.

The method finally settled on was to test each quantity of bouillon prepared in the laboratory. If any failed to give rise to gas in the fermentation tube it was set aside to be used exclusively with these tubes. Unfortunately most of the gas-production recorded in the tables following, took place in bouillon containing traces of glucose since the work could not be delayed. The difficulty has been partly overcome by keeping a record of the quantity of gas formed in the same bouillon to which no sugar was added.

In searching through the literature of this subject I find that the presence of glucose in bouillon has likewise been noted by Peré[7] and by Pane[8] in its bearing on the products of bacteria fermentation. The former considered it mainly in its relation to the initial acidity of cultures, a relation, to which I had already called attention in 1890[9]. Pane sought to determine the gas produced in peptone bouillon quantitatively by noting the number and the size of the gas bubbles in bouillon-agar when *B. coli communis* was mixed with fluid agar and this rapidly hardened by cooling. He likewise determined the amount of acid produced by the fermentation of this carbohydrate.

TYPES OF GAS PRODUCTION.

In my experience with the cultivation of bacteria in the fermentation tube a variety of hitherto unnoticed details have come to light. In arranging and classifying these I find more or less difficulty. It seemed perhaps the simplest plan to describe the gas production of a very common and much discussed species—*Bacillus coli communis*—and then to refer briefly to those species which belong to the same general group. The observations of others so far as they bear on the subject before us will be reviewed in a succeeding chapter.

B. coli communis.—It is not my intention to enter into detail concerning the characters of this somewhat notorious intestinal species. At present its main differential characters are accepted to be 1, motility; 2, prompt coagulation of milk; and, 3, gas production in nutrient media containing lactose.

As regards motility it is interesting to note that it is more easily overlooked in bouillon cultures than when very recent colonies on gelatin or agar are examined in the hanging drop. There is moreover a considerable variation among cultures from different sources as to this property of motility. There are to be found all gradations from cultures in which a motile form may be seen only after prolonged searching, to those in which almost all individuals are in motion. As to the coagulation of milk there is likewise some variation in this function. Some years ago I isolated an unquestionable colon bacillus from the feces of an infant, which failed to produce coagulation of milk even after several weeks' sojourn in the thermostat. The same may be said of some cultures from animals. These facts show that the colon bacillus is by no means a well characterized species and the question arises how shall the various races be classified? The same thoughts have been expressed by other writers especially by Gilbert and Leon[10]. I believe that the properties of these races as manifested in the fermentation tube will serve as the best basis for a classification.

If we take for our culture a bacillus isolated from human feces and manifesting all the characters usually ascribed to *B. coli communis* we shall observe the following phenomena in the fermentation tube at 37° C.

In glucose bouillon within twenty-four hours the entire fluid has become clouded and a certain quantity of gas has accumulated in the closed branch. At the end of the second day more gas has formed. At the end of the third day a trifle more is present. After this very little if any is set free. The cloudiness promptly subsides and all growth is apparently at an end. The fluid in the bulb will be found markedly acid. This acidity is undoubtedly the cause of the sudden cessation of activity, for if it be promptly neutralized with a sterile solution of some alkali the fermentation starts again. It should be stated that in these observations no "acid-binding" substance, such as $CaCO_3$ has been added to the fermenting fluid. The following table gives in percentages of the tube length of the closed branch (*i. e.*, of the volume of the latter) the amount of gas formed by *B. coli* from various sources:

II.—*B. coli communis* in Glucose Bouillon. (Fig. 2 of Plate.)

B. coli communis.	Gas accumulated at the end of				CO_2.	H.
	1 day.	2 days.	3 days.	9 days at 20°–25° C.		
	pr. ct.	pr ct.	pr ct.	pr ct.	pr ct.	pr ct.
1. From human feces	46	58	62	57	37.2	62.8
2. " " "	30	45	54	45 (6th)†	37	63
3. " cattle.	44	52	62	58	37.2	62.8
4. " swine.	36	42	44	46	33	67
5. " water.	28	44	47	44	32	68
6. " "	34	47	54 (5th)†	45	31.5	68.5
7. B. of Grouse disease (Klein)*	43	51	53	51 (6th)†	34	66

* This culture came thus labeled from Kral's collection in Prague. It corresponded closely with Klein's description of the bacillus isolated by him from the organs of diseased grouse[1]. I include it in this table because it resembles *B. coli* in many respects and its action on the sugars is vigorous and equal to that of any variety of *B. coli* here represented. A comparison of the gas production in glucose, lactose and saccharose bouillon shows this function to be identical in character in all three.

† The figures refer to the number of days after inoculation of the culture fluid.

From the foregoing table it will be seen that the largest amount of gas is produced during the first twenty-four hours and that the gas itself is made up of CO_2, one volume, to an explosive gas, two volumes. During the past five years I have examined a large number of cultures of *B. coli* which I isolated from the intestinal contents of domesticated animals

and in every case this ratio of CO_2 to H was the same. The somewhat crude method of measuring the gas, the contraction of its volume when removed from the thermostat, the fluctuating temperature of the room, the presence of a layer

III.—*B. coli* IN LACTOSE BOUILLON. (Fig. 3 of Plate.)

B. Coli communis.	Gas accumulated at the end of							CO_2.	H.
	1 day.	2 days.	3 days.	4 days.	5 days.	6 days.	Total at 20°–25° C.		
	pr ct.	pr ct.	pr ct.	pr ct.	pr ct.	pr ct.	pr ct.	pr ct.	pr ct.
1. From human feces . . .	55	62	64	. . .	. . .	. . .	61 (6th)	37	63
2. " " " .	28	42	45	48	. . .	52	45 (8th)	37	63
3. " cattle . . .	39	44	46	. . .	51	. .	50 (8th)	40	60
4. " swine . . .	51	56	60	. . .	. . .	61	56 (7th)	36.7	62.3
5. " water . . .	60	65	. . .	. . .	. . .	66	60 (7th)	. . .	. . .
6. " " . . .	33	51	56	. . .	. . .	64	59 (11th)	40.5	59.5
6.* " " . . .	24	34	44	48	50	. . .	48 (8th)	35	65
7. B. of Grouse disease	42	58	62	. . .	. . .	. . .	60 (11th)	33.8	66.2

* Bouillon entirely free from muscle glucose. Culture made six months after the first.

of foam on the surface of the liquid in the closed branch after the CO_2 has been absorbed, all these factors enter as slightly disturbing elements and make the values quoted as only approximately correct. As might be anticipated from the

prompt precipitation of the casein in milk inoculated with *B. coli*, this organism acts upon lactose in the same way as upon

IV.—*B. coli* IN SACCHAROSE BOUILLON. (Fig. 4 of Plate.)

B. coli communis.	Gas accumulated at the end of							Total gas at 20°-25° C.	Reaction of bulb.	CO_2	H
	2 days.	4 days.	6 days.	7 days.	9 days.	12 days.					
	pr ct	pr ct	pr ct	pr ct	pr ct	pr ct				pr ct	pr ct
1*	22.4	30	56	63	. . .	41 (11th)		60 (11th)	acid	38	62
1.	16	. . .	. . .	26	31	58 (13th)		65 (29th)	alkal.	43.5	57.5
2	21	38	46	. . .	53	. . .		63 (20th)	acid	37	63
3	. . .	. . .	. . .	. . .	bubble	. . .		. . . . .	alkal.	. . .	. . .
4	18	21	26	27	32	36		46 (18th)	acid	38.2	61.8
5	31	47	50	. . .	. . .	. . .		43 (11th)	"	36.5	63.5
6†	7	13	15	16	20(8th)	. . .		19 (10th)	alkal.	23	77
6†	. . .	. . .	. . .	14	. . .	. . .		13 (10th)	"	20	80
7 (Grouse disease)	47	50	. . .	. . .	. . .	. . .		50 (6th)	acid	35.5	64.5

* These figures correspond to those of the cultures in tables II and III.
† Much of the gas set free by this bacillus must be ascribed to muscle glucose.

glucose and the phenomena in the fermentation tube containing lactose bouillon are precisely the same as those in glucose bouillon.

The action of *B. coli* on cane sugar in peptone bouillon dif-

fers with rare exceptions, quite markedly from that upon glucose or lactose. The examination of cultures from different sources has revealed two distinct varieties, one of which produces a considerable quantity of gas, the other little or none. With the former variety the type of gas production varies somewhat from culture to culture. In general the fluid is driven out very slowly and the gas production may last several weeks. These statements are well illustrated in table IV.

When the gas production goes on very slowly the growth in the open bulb becomes exceedingly abundant. This is most probably due to the slow neutralization of the bacterial alkali, formed in the open bulb, by the acid resulting from the slow fermentation in the closed branch. The gradual entrance of this acid fluid into the bulb acts as a continuous stimulant to the multiplication of bacteria there. When the gas production is rapid the fluid in the bulb remains acid and the growth speedily subsides.

What the true significance of the varying behavior of the *B. coli* group towards cane sugar is, can be determined only by more extended investigations. I venture to suggest however, that the saccharose fermentation may require in the slow fermentation the presence of an inverting ferment while that of lactose and glucose goes on without it. This ferment is apparently no longer formed by some bacteria otherwise not distinguishable from *B. coli*. The whole subject is very interesting and seems to indicate either that this species may readily lose the capacity to act on cane sugar or else that it is in a transition stage towards the more pathogenic species of this large group of bacteria. The peculiarity of the saccharose fermentation suggests the thought that the presumable ferment is formed only in the fluid in contact with oxygen and that it very slowly diffuses thence into the closed branch. A layer of sterile oil on the fluid of the bulb would perhaps answer this question. But I have had no opportunity to try this expedient. We may summarize the facts concerning the gas-producing power of *B. coli communis* briefly as follows :—

In feebly alkaline peptone bouillon containing 2 per cent. of glucose or lactose, about 50 to 60 per cent. of the closed branch of the fermentation tube will be occupied by gas in 3 or 4

days and the fluid will be strongly acid. The gas is composed of about 2 volumes of H and 1 volume of CO_2. In bouillon containing 2 per cent. cane sugar the gas production goes on in cultures of some varieties. It accumulates more or less slowly and the ratio of CO_2 to H varies.*

The Hog-cholera Group of Bacilli.—While forms differing more or less in physiological and cultural features are thrown together as *B. coli communis*, pathogenic forms having much closer affinities, in fact scarcely any points of difference, are carefully separated and named. This anomaly is due to the practical importance of pathogenic species. Of the hog cholera bacillus itself, an organism of considerable economic importance as well as of marked pathological interest, I have examined in the course of the past seven years a number of cultures from widely different regions of our country. Some of these possessed minor varietal characters, among which may be included a considerable variation of pathogenic power. With a few exceptions the gas producing phenomena are remarkably uniform. In case of these exceptions, one of them a culture now seven and a half years old, the gas production is somewhat reduced quantitatively. Whether this is an original peculiarity or a result of prolonged cultivation I am not prepared to state.

They all possess the power of fermenting glucose in precisely the same manner as *B. coli*, but they are incapable of producing gas in bouillon containing cane sugar and milk sugar. The absence of any action on milk sugar in this group is correlative with the absence of any power to coagulate milk. Even after weeks of sojourn in the thermostat and subsequent boiling, milk cultures remain fluid. In this group I also include a still unnamed bacillus from the genital passages of a mare, *B. enteriditis*, Gärtner[14], and *B. typhi murium*, Löffler[15]. These are the only ones which I have carefully examined. There are probably others, found in different countries, which belong to this group of pathogenic bacteria.

In the following table are included several distinct physiological varieties of the hog cholera bacillus :—

* The products of the fermentation induced by *B. coli* have been more or less exhaustively studied by Baginsky [6], Peré [7] and Scruel [8].

V.—Hog Cholera Group of Bacilli in Glucose Bouillon.

Species.	Gas present after				Total at 20°–25° C.	CO_2.	H.	Remarks.*
	1 day.	2 days.	3 days.	4 days.				
	pr ct.	pr ct.	pr ct.	pr ct.	pr ct.	pr ct.	pr ct.	
B. choleræ suis, I	22	35	37	40	37	34	66	Culture 7½ years old.
" " " II	35	51	56	58	54	37	63	Culture 3 years old.
" " " III	45	58	58	58	52	36	64	Feebly pathogenic variety ; 4 years old.
" " " IV . . . . . (Swine pest.)	33	43	45	45	42	33	67	Culture probably 6 years old.
Bacillus from mare	12	50	58	61	55	36.5	63.5	Culture 2 years old.
B. typhi murium (Löffler,) . .	. . .	46	48	. . .	50 (8th)	35	65	Culture probably 2 years old.
B. enteriditis (Gärtner,) . . .	. . .	49	52	. . .	52 (8th)	30	70	Culture probably 5–6 years old.

* The age here indicated refers to the time which has elapsed since the species was obtained from a case of disease, or since it was discovered.

I have omitted from the above record four additional cultures of *B. choleræ suis*, three of which are identical with II and III so far as the quantity of gas produced is concerned; the fourth corresponds to IV in this respect. In all varieties of this sub-group the behavior in glucose bouillon is precisely the same. There is a rapid evolution of gas on the first and the second day ceasing promptly on the fourth or fifth. The growth subsides at the same time. The culture fluid becomes strongly acid.

The action of this entire group on saccharose and lactose in bouillon is negative and hence I omit any tabulation of the records. Unless the bouillon is free from muscle glucose there may have accumulated, after one or two weeks, a certain amount of gas corresponding to that developed in the same bouillon free from any additions. This may amount to 15 or 20 per cent. of the contents of the closed branch. A glucose-free bouillon recently tried remained free from any gas. That there is, in such tubes, no action on the sugar is proven by the feeble transitory acid reaction when gas is formed to a slight extent. This soon changes to an alkaline reaction in the bulb. When glucose is entirely absent the acid reaction fails to appear.

B. lactis aërogenes Escherich[3]. The cultures which I have tested differ from those of *B. coli* in certain minor but definite characters. They were non-motile and provided with more or less zooglœar or intercellular, but not viscid, substance often recognizable on the border of the hanging drop as a distinct capsule. When these bacilli are cultivated on solid media this capsular substance manifests itself by a regular spacing between the individual bacilli when these are massed together. The growth on potato is richer and of a paler yellow color than that of *B. coli*. The surface colonies on gelatin are usually fleshier than those of the latter and frequently resemble little pearly drops. In old bouillon cultures there is noticeable an even stronger fecal odor than that arising from similar cultures of *B. coli*. I give the above characterization mainly because the species does not seem to be any more stable in its minor characters than *B. coli*. The following table gives the gas production of the only culture thoroughly examined.

It will be noticed that saccharose is not affected. The gas formed was traced to muscle glucose in the bouillon.

VI.—*B. lactis aërogenes* IN SUGAR BOUILLON.

Kind of Sugar.	Gas present after					Total at 70° F.	CO_2	H	Remarks.
	2 days.	3 days.	4 days.	5 days.	6 days.				
Glucose . .	41	54	. . .	. . .	. . .	50 (11th)	35	65	Growth subsided; acid.
	60*	. . .	. . .	. . .	. . .	58 (7th)	. . .	. . .	" " "
Lactose . .	45	61	63	66	68	62 (11th)	38.5	61.5	" " "
	40*	47	50	. . .	52	53 (14th)	38.7	61.3	" " "
Saccharose	8	9	11	13	. . .	13 (11th)	6	94	Growth abundant; alkaline.
	8*	12	. . .	. . .	15	17 (13th)	20	80	" " "

* The second trials with the same kind of sugar were made fully half a year after the first.

The fermentation in so far as the gas production is concerned is precisely similar to that of the entire *B. coli* group.

Some years ago[16] I examined comparatively three slightly different bacteria obtained from the intestines of the pig. One of these corresponded very closely to the species above described but differed from it in producing an abundance of gas in saccharose bouillon. We probably have a number of

VII.—BACILLUS OF FRIEDLÄNDER.

SUGAR.	Gas accumulated after							Total gas at 20°–25° C.	Reaction of bulb.	CO_2.	H.
	2 days.	3 days.	4 days.	9 days.	10 days.	11 days.					
	pr ct.	pr ct.	pr ct.	pr ct.	pr ct.	pr ct.		pr ct.	pr ct.	pr ct.	pr ct.
Glucose . .	41	45	. . .	. . .	. . .	. . .		43 (7th)	acid.	32.7	67.3
Saccharose	35*	42	46	. . .	. . .	. . .		46 (9th)	acid.	32.8	67.4
	36†	40	43	46(6th)	. . .	. . .		45 (8th)	acid.	34.6	65.4
Lactose . .	6*	12	15	17	21	24		23 (17th)	alkal.	14.3	85.7
	trace.†	4	8	11	13	. . .		13 (10th)	feebly acid	trace.	nearly 100

* Bouillon containing a trace of muscle sugar, (H of table I.)
† Bouillon containing no muscle sugar, (I of table I.)

varieties which may be grouped under the specific name *B. lactis aërogenes* and which further fermentation studies may tend to define and separate. There is furthermore good reason for regarding this species very closely related to *B. coli.*

The bacillus of Friedländer*. This species has aroused considerable attention owing to the supposition prevailing at one time that it was the cause of pneumonia in man. With reference to both morphological and cultural characters it seems to bear the same relation to *B. lactis aërogenes* which the hog cholera bacillus bears to *B. coli.* From the above table it will be seen that this organism acts vigorously upon glucose and saccharose but only feebly on lactose.

The persistence of the gas-producing function of this species is well illustrated by the fact that three years ago the same culture gave the following result[16]:

Glucose,	total gas 44 pr. ct.;	CO_2 43.4 pr. ct.,	H=56.6 pr. ct.
Saccharose,	" " 46 " "	" 41 " "	H=59 pr. ct.
Lactose,	" " 19 " "	" 21.8 " "	H=78.2 pr. ct.

B. œdematis maligni. Of anaërobic species only a few have been cultivated in the fermentation tube. Some of these were derived from the bodies of animals and represented those "post mortem" bacilli quite invariably present some time after death especially in the carcasses of large animals. These were found gas-producing but no record was kept. In 1890[18] I isolated an anaërobe, probably identical with the bacillus of malignant œdema, from the organs of a pig. I append a somewhat incomplete record of gas production in the fermentation tube studied at that time which indicates a close relationship to the same process in the *B. coli* group:

* This bacillus has been studied from the chemical aspect by Frankland, Stanley and Frew[17].

VIII.—*B. œdematis maligni.*

Glucose.				Lactose.		Peptone bouillon without sugar.		Saccharose.	
Time required.*	Total gas	CO_2	H	Time required.	Total gas.	Time required.	Total gas.	Time required.	Total gas.
	pr ct	pr ct	pr ct		pr ct		pr ct		
12 days	80	31	69	3 days	80	4 days	4	2 days	0
13 "	60	33	67	. . . . .	. . .	. . . . .	. . .	. . . . .	. . .
12 "	63	34	66	. . . . .	. . .	. . . . .	. . .	. . . . .	. . .
8 "	86	. . .	. . .	. . . . .	. . .	. . . . .	. . .	. . . . .	. . .

*The notes do not state whether the total quantity of gas had not been formed before the time indicated.

Proteus vulgaris. This species has certain points of contact as regards morphology with the *B. coli* group. It differs in possessing very active peptonizing properties as manifested in gelatin. Its power of gas production is peculiar in that a smaller quantity of gas is formed than in cultures of *B. coli.* It likewise is peculiar in being unable to produce gas in lactose bouillon while its action in glucose and saccharose bouillon is the same. Repetition of the gas test at intervals and with

subcultures which had lost almost completely the peptonizing power gave the same result.

IX.—*Proteus vulgaris.*

Sugar used.	Gas present after						Reaction of bulb.	CO_2	H
	1 day.	2 days.	3 days.	5 days.	7 days.	Total at 70° F. in 9 days			
	pr. ct.	pr. ct.	pr. ct.	pr. ct.	pr. ct.	pr. ct.		pr. ct.	pr. ct.
Glucose . .	4	20	28	—	35	31	Acid	28	72
Lactose . .	2	5	—	8	10	10	Alkaline	Trace	Nearly 100
	0*	0	0	0	—	—	"	—	—
Saccharose.	6	20	30	34	36	33	Acid	39	61
	—*	24	36	32	33 (6th)	32 (6th)	"	33⅓	66⅔

* Bouillon I of Table I containing no muscle glucose. The rest is bouillon H, containing a trace.

The Bacillus-Cloacæ Type of Gas Production.—The types of gas production hitherto described present certain underlying characters which suggest a close relationship. These I group together as the *B. coli* type since it differs quite markedly from the type now to be described.

The species known as *B. cloacæ* was first described by E. O. Jordan[19] as coming from sewage. The cultures which I have ranged under this name have been obtained, with one exception, from water both polluted and unpolluted. The exception was reputed to have come from cornstalks. It is therefore a widely diffused organism whose true habitat I do not know, although I am strongly of the opinion that it is an organism living on decaying vegetable matter. If so, its name is unfortunate as it could not be regarded as a sewage bacterium strictly speaking. It is a small bacillus closely resembling *B. coli* in form and size and is actively motile. On gelatin the surface colonies appear at first as thin expansions with slightly irregular outline. Two or three days after the colonies have appeared, liquefaction sets in. This peculiar retardation of liquefaction is noteworthy and in general, it may be said, that the rapidity varies slightly from culture to culture and is gradually weakened during artificial cultivation. Milk I find coagulated only after seven or eight days. On potato a fleshy, pale yellowish, not characteristic growth appears after one or more days. I may state here that two varieties of this species have come under my observation which I designate provisionally α and β. For α, the bouillon becomes uniformly turbid, for β very feebly so with a tendency of the growth to form flakes somewhat like the flocculi of anthrax cultures. Evidently there is in β a greater tendency towards cohesion of the bacilli.

The gas production of *B. cloacæ* is very rapid in glucose and saccharose bouillon and slow in lactose bouillon.

X.—*B. cloacæ*, (Figs. 5 and 6 of Plate.)

Bacillus.	Amount of gas accumulated after					Reaction.	H.	CO_2.
	1 day.	2 days.	3 days.	4 days.	Total 20°-30° C.			
α.	pr ct.	pr ct.	pr ct.	pr ct.	pr ct.		pr ct.	pr ct.
Glucose . .	32	77	. . . .	96	96 (4th)	faintly acid	30	70
Saccharose	70	95	. . . .	. . . .	86 (4th)	faintly acid	42	58
Lactose . .	15	20	. . . .	25	60 (22d)	alkaline	63.4	36.6
β.								
Glucose . .	. . . .	. . . .	73	78	82 (6th)	. . . . .	31.6	68.4
Saccharose	2	33	49 (4th)	73 (5th)	95 (7th)	acid.	25	75
Lactose . .	. . . .	20	. . . .	37	80 (10th)	acid.	46.5	53.5

This type of gas production differs from the *B. coli* type : 1, in the much greater accumulation of gas which drives out all of the fluid from the closed branch in two or three days ; 2, in the much larger proportion of CO_2, the fraction $\frac{H}{CO_2}$ varying from ½ to ⅓ ; 3, the much feebler acid reaction of the fluid in the open bulb. The lactose fermentation goes on at a slow steady pace and after one or two weeks a considerable quantity of gas has accumulated in which the relative quantity of CO_2 and H varies considerably.

The behavior of *B. cloacæ* in the fermentation tube reminds us of the action of ordinary yeast under the same conditions. There is in both the same rapid evacuation of fluid from the closed branch. The fundamental difference between the two processes, however, is the invariable presence of H in cultures of the bacterium.

XI.—*Saccharomyces cerevisiæ* (Fig. 7 of Plate.)

Sugar.	Gas accumulated after							Reaction.	CO_2	H
	2 days.	3 days.	4 days.	5 days.	6 days.	7 days.				
	pr ct	pr ct	pr ct	pr ct	pr ct	pr ct			pr ct	
Glucose	21	63	. . .	100	. . .	. . .		neutral	100	. . .
Saccharose	0	3	27	50	83	96		acid	100	. . .
Lactose	0	0	0	0	0	0		alkaline, growth very feeble	. . .	. . .

Among the more important bacteria which have been tested in the fermentation tube and which fail to set free any gas may be mentioned the following:

Staphylocci.

Streptococci.

Septicæmia hæmorrhagica (rabbit septicæmia, swine plague, fowl cholera, *Wildseuche*, etc.)

B. typhi abdominalis.

The various comma bacilli (*Spirillum chol. Asiat.; Sp.* Deneke, Finkler and Prior, Smith.)

B. anthracis.

Many aërobic spore-bearing bacilli.

B. mallei.

Concerning that strictly aërobic species, *B. subtilis*, Vandevelde[10] finds, contrary to earlier determinations of Prazmowski[11], CO_2 and H given off in varying quantities. Obviously the former worked with impure cultures. The absence of gas production in cultures of *B anthracis* was pointed out by Arloing[4] in 1886.

SOME GENERAL OBSERVATIONS ON THE PRODUCTION OF GAS BY BACTERIA AND ITS RELATION TO THE FORMATION OF ACIDS IN THE CULTURE FLUID.

A consideration of the results obtained with the fermentation tube develops a number of interesting phases of bacterial life. Perhaps the most important fact to be gathered is the fundamental character of gas production not only in distinguishing species but groups of species. The phenomenon of fermentation as expressed by gas production may in fact be called a group reaction. It is, for example a common character of a large group of motile bacteria which we may designate the *B. coli* group. While it is absent in other equally large and important groups such as *Septicæmia hæmorrhagica* and the comma bacilli. I regard, therefore, the production of gas not as one of the large number of minor differential characters by which we are in the habit of fixing a species but as one of fundamental importance, associated with groups of bacteria having perhaps a common phylogenetic origin.

In view of the presumable importance of gas production* the question may be asked as to the permanence of this function. The permanent or temporary character, under cultivation, must largely decide for or against the position taken above as to the fundamental importance of kinds of fermentation in the grouping of bacteria. The facts which I have collected are necessarily meager since I have employed the fermentation tube only for four years, and no other person has thus far paid any attention to this subject. A few facts, however, bear on this point. I have not yet encountered any bacteria which have either gained or lost the gas-forming function under cultivation. In the colon group it does not appear to vary at all from year to year. The same persistence was observed in *Proteus vulgaris*. Of two varieties originally descended from the same colony, one still actively liquefying gelatin, the other having lost this power almost absolutely, both produce the same amount of gas in glucose and saccharose bouillon. Recently I have noticed in one of the cultures of *B. cloacæ*, over a year old, a slight diminuition in the total quantity of gas set free in saccharose bouillon. In glucose bouillon the function seems to be intact. While, therefore, the power of gas production may be slightly reduced quantitatively it does not disappear. It likewise is, at least for *Proteus vulgaris*, a much more permanent function than that of secreting a liquefying ferment.†

More or less related to an enfeeblement of the fermenting power observed in the space of months and years in the same culture, is an incapacity probably the result of an adaptation to a parasitic existence. This is very well illustrated by the

* I simply use this word as standing for types of fermentation which need more careful examination by chemists than they have hitherto received.

† In opposition to my observations is one recorded by Arloing[1]. A *micrococcus septicus puerperalis* (probably a streptococcus or a staphylococcus) produces no gas when fluids containing sugar are inoculated from old cultures. When, however, young cultures twenty-four to thirty-six hours old are used for inocculation, CO_2 and H are given off abundantly. Such a remarkable change of function must rest upon some experimental error of the author.

colon group which may be divided into a saprophytic and a parasitic sub-group as follows:

A. Saprophytic sub-group.
  1a. Ferment all three sugars with same rapidity. . . Bacillus of grouse disease and some colon bacilli.
  1b. Ferment glucose and lactose rapidly, saccharose slowly. . . . *B. coli* α (1a and 1b).
  2. Ferment glucose and lactose rapidly, saccharose not at all. . . . *B. coli* β.
B. Parasitic sub-group.
  1. Ferment glucose rapidly, saccharose and lactose not at all. . . . all pathogenic forms.

I am inclined to associate this loss of functional activity in the pathogenic group B with an adaptation to a more parasitic existence and the development of certain other powers—the formation of toxic substances perhaps—which enables them to live in competition with living tissues while they have largely forfeited their power to compete with the more saprophytic forms from which they may have originally sprung.

It might be claimed that the phylogenetic loss of gas production is simply a change in the kind of fermentation, from the butyric to the lactic for example. That this is not true can be readily demonstrated, for in saccharose and lactose bouillon, when muscle glucose is absent and no gas appears in consequence, the reaction of the bouillon does not become acid. Among those bacteria which act upon sugars without the development of gas, a strongly acid reaction appears within twenty-four hours. The failure of the group B to act upon lactose is furthermore shown by their inability to produce coagulation of milk. We have, therefore, no ground for assuming a change in the type of fermentation. It is an absolute loss of function and not a modification.

In bringing together the more detailed observations on gas production a certain number of interesting facts claim our attention. We note that in the *B. coli* type of gas production in glucose only a certain quantity of gas collects—45 to 60 per cent. of the capacity of the closed branch—while in the *B.*

cloacæ type fully 100 per cent. is formed. Again the fraction $\frac{H^*}{CO_2}$ for *B. coli* is approximately $\frac{4}{1}$ while that for *B. cloacæ* is $\frac{1}{2}$ or $\frac{1}{3}$. The reaction of the fluid in cultures of the latter is feebly acid while for the *B. coli* group it is always strongly acid. Grimbert[21] in his studies of an anaërobic organism ascribes the greater production of CO_2 to a greater formation of alcohol and the more abundant production of H to a greater formation of acid in accordance with the following formulæ:

$$C_6H_{12}O_6 = C_4H_8O_2 + 2CO_2 + 4H \therefore \frac{H}{CO_2} = \frac{50}{50}$$

$$C_6H_{12}O_6 = C_4H_{10}O + 2CO_2 + H_2O \therefore \frac{H}{CO_2} = \frac{0}{100}$$

This would agree well with the feebly acid reaction of cultures of *B. cloacæ* and the strongly acid condition of those of *B. coli*.

Another phenomenon constantly observed is the great predominance of H over CO_2 in either type when only a little gas has been formed as in peptone bouillon containing traces of muscle sugar. The same phenomenon is noticeable when the gas at different stages of the process is examined. This may be illustrated by the three following stages in the gas production by *B. cloacæ*.

After 22 hours 37.5 per cent. gas has accumulated; CO_2, 46.6 per cent.; H, 53.4 per cent.

After 22 hours† 73 per cent. gas has accumulated; CO_2, 61 per cent.; H, 39 per cent.

After 96 hours 95 per cent. gas has accumulated; CO_2, 70 per cent.; H, 30 per cent.

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* We should not ascribe more than a comparative value to this fraction for the reason that Co_2 is much more soluble in water than H. Thus at 20° C. one volume of water takes up 0.9014 volumes of CO_2 and only .0193 volumes of H. If we bear in mind that at the beginning of fermentation a comparatively large quantity of CO_2 may become absorbed in the bouillon the relation of CO_2 to H in the fermentation tube will be understood to be entirely different from the ratio obtained by exact analytical methods.

† A second tube inoculated with the first but having produced gas more promptly.

I have been inclined to ascribe this to the absorption of CO_2 by the bouillon but Grimbert[22] as well as Frankland[17] finds by exact quantitative determinations of the gases the same increase of CO_2 as the fermentation progresses. The former explains it by assuming a greater production of alcohol in the later course of the process in accordance with the formulæ given above. According to this explanation the type of fermentation of *B. cloacæ* may differ from that of *B. coli* simply by an increased production of some alcohol at the expense of an acid. If we go a step farther and bring within the range of comparison another type of gas production, that of ordinary yeast by which only CO_2 and ethyl alcohol are produced (if we neglect traces of succinic acid) we have eliminated both the hydrogen and the acid element which seem to go together.

A farther point of interest is the constant presence in all cultures examined of an inflammable, explosive gas which I have assumed to be hydrogen. Most observers, including Arloing[4], Escherich[7], Frankland[17], Peré[7], Scruel[18], Grimbert[22], and others report only CO_2 and H. Baginsky[12] on the other hand claims the presence of CH_4 as well. It would be interesting to determine whether bacterial fermentation ever goes on without the evolution of both CO_2 and H at the same time.

In examining the action of bacteria on the three sugars used, we note that the gas production in glucose bouillon is always rapid though it may be slow or absent in lactose and saccharose bouillon. Glucose is thus the sugar most easily acted upon. A curious preference is shown by certain species for certain sugars. Thus *B. coli* produces gas rapidly in lactose and slowly or not at all in saccharose bouillon. Friedländer's bacillus on the other hand, acts vigorously upon saccharose and very slightly upon lactose. The latter is not touched by *Proteus vulgaris* at all. By pushing such comparative inquiries still farther and including other carbo-hydrates, as has been done by most of the authorities cited above from a slightly different point of view, still finer lines of distinction might be drawn. Owing to lack of time I have not

gone beyond the three sugars noted excepting to test some species in potato starch suspensions several years ago.*[16]

The source of the two gases CO_2 and H may be explained by the old formula of the text-books which splits one molecule of grape sugar into two of lactic acid and these into one of butyric acid and two each of CO_2 and H. This formula demands equal volumes of these gases. Scruel holds that the molecule of glucose breaks up into one of formic, of acetic, and of lactic acid with fixation of one atom of O. The gases he derives from the direct decomposition of the newly formed molecule of formic acid:

$$CH_2O_2 = CO_2 + H_2.$$

As has been recently emphasized by Grimbert and stated above, the process of fermentation varies from beginning to end so that no single equation can express more than what is going on at any one time. The same author ascribes this continual change to a modification of the vitality of the ferment organism brought about by the accumulation of harmful products in the fluid.

The rapid evolution of gas in the presence of one kind of sugar and its slow accumulation in the presence of another brings up the question whether or not an inverting ferment comes into play in the slow fermentation. This question is not approachable by the simple methods I have employed. It is certainly a curious fact that one bacterium may produce gas with almost equal rapidity in three sugars, another in two and that these two may be, with one species, glucose and saccharose, with another, glucose and lactose. Thus the bacillus of grouse disease produces gas in glucose, lactose and saccharose with equal rapidity.

Bacillus coli produces gas in glucose and lactose with equal rapidity. Action on saccharose variable.

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*The action of bacteria on potato starch may be demonstrated by cutting potatoes so that they fit rather snugly into test tubes. The film of water between them and the glass imprisons any gas bubbles that may be set free. In this way I noted the evolution of gas in several species, among them Friedländer's bacillus.

The bacillus of Friedländer produces gas in glucose and saccharose with equal rapidity. Very slight action on lactose.

Proteus vulgaris produces gas in glucose and saccharose with equal rapidity. No action on lactose.

Bacillus cloacæ produces gas in glucose and saccharose with equal rapidity. Action on lactose slow.

The probability of the direct breaking up of the molocule of saccharose and lactose[5] without inversion, has been affirmed by nearly all recent authorities and seems plausible when gas accumulates very rapidly as in cultures of *B. cloacæ*. It is evident that the observatious made with the fermentation tube open some very interesting problems, the solution of which must be left to others.

In connection with the selective action on sugars manifested by different species seemingly related to each other the thought has occurred to me that a clue to the habitat of bacteria might be obtained by an investigation of their predilections. Inasmuch as there are certain products such as lactose peculiar to animals, and certain others, such as saccharose peculiar to plants an adaptation to one or the other carbohydrate would indicate a saprophytic existence on animal or vegetable products. This hypothesis however needs a larger array of facts than I am able to put together, to prove or disprove its correctness.

The production of CO_2 and H together with other gases during the decomposition of proteid substances has been affirmed by Kerry[23] and Bovet[24]. The former used carefully prepared serum-albumin, the other serum-albumin and yolk of eggs. In the accurate determination of the source of gas production in putrefactive processes, it is evident that carbohydrates must be carefully eliminated since the fermentation of these substances with evolution of CO_2 and H seems to be such a wide spread function among bacteria.

There is one other phase of the subject of fermentation which has an important bearing upon bacteriology. I refer to the formation of acids* which seems to be clearly traceable

* Thus in milk cultures of *B. coli*, Baginsky[12] found formic, acetic, aud lactic acids. The same were found by Scruel. Peré[7] detected acetic and lactic acid. Frankland, Stanley and Frew[17] determined, in cul-

to the presence of carbo-hydrates. Some years ago, Petruschky[25] examined the acid and alkali-producing functions of bacteria by using as a culture medium specially prepared whey from milk. I called attention to the fact that such classification had only a limited value since it depended entirely on the composition of the culture fluid[9]. The whey, having as an important ingredient, lactose, would prove only such bacteria acid-producing which were able to cause fermentation of the milk sugar while those which could not do this would show themselves as alkali producers. Bearing on this subject are the statements made by bacteriologists in the early days of this branch of biology that cultures of many bacteria are at first slightly acid before becoming alkaline. I suggested that this was probably due to traces of sugar in the culture fluid and I was able to prove this by causing an oscillation from an acid to an alkaline reaction and back again by adding at intervals small quantities of glucose to the bouillon. The alkali formed during the multiplication of bacteria was neutralized by the acid derived from the fermentation of the glucose. If this was small in quantity the acid or acids were formed in correspondingly small quantities and the alkaline reaction soon reappeared. I was able to show furthermore that the addition of small quantities of fermentescible sugar greatly favored the multiplication of bacteria by keeping down the alkaline reaction. After I began testing peptone bouillon for muscle glucose with gas-producing bacteria, I found that in bouillon free from sugar the multiplication of various acid producing bacteria such as streptococci, staphylococci, *B. typhosus*, *B. diphtheriæ*, *B. coli*, and *B. choleræ suis* is not attended with any acid reaction, either temporary or permanent.

So far as my observations have gone they show that all bacteria are alkali producers in bouillon free from carbo-hydrates, and that when one or the other of this group is present a very large number of the most easily cultivated bacteria are acid producers. This two-fold activity probably serves a useful purpose in keeping the medium in which they live more or

tures of the bacillus of Friedländer ethyl alcohol, acetic acid and a little formic and succinic acid. Grimbert[82] detected among the products of *B. orthobutylicus* normal butyric alcohol, butyric and acetic acid.

less neutral and therefore favorable to their continued multiplication. A good illustration of this fact is afforded by the growth of *B. coli* in saccharose bouillon. The gas production goes on (with most varieties) very slowly. The fluid in the bulb in contact with the air becomes alkaline and very turbid with growth. The fluid in the closed branch becomes acid under the influence of the slow fermentation and remains so. As it is gradually pushed out into the bulb by the slow accumulation of gas it tends to reduce, by degrees, the alkalinity of the fluid therein contained and thus favors step by step, the growth which finally becomes very dense.

The employment of sugar as a constituent of culture media is therefore, a matter of considerable importance. For certain species, like *B. coli* for instance, the addition of 1 per cent. glucose or lactose would be a decided detriment to the culture and soon lead to its destruction. Cane sugar on the other hand, added in the same proportion, would favor the growth owing to its much slower decomposition. Again the addition of very small quantities of glucose from time to time is favorable as stated above. In fact, bouillon, entirely free from muscle glucose, is less desirable than that containing traces, and in general it would be well to add glucose to bouillon. The limit may safely be put at 0.1 per cent. These remarks apply equally well to the large group of bacteria which produce acids in sugar solutions without the evolution of gas and in searching for the most favorable media for any species its behavior toward the more common carbo-hydrates should be carefully looked into.

APPLICATION OF THE FERMENTATION TUBE TO PROBLEMS IN PRACTICAL SANITATION. THE GAS TEST IN THE DIFFERENTIATION OF B. TYPHOSUS FROM THE B. COLI GROUP OF BACTERIA.

The use of the fermentation tube as an important differential test in bacteriology led me in 1889 to compare the frequently confounded species, *B. typhosus* and *B. coli communis*. A sharp distinction was at once detected between them which manifested itself by a total lack of gas production on the part

of the typhoid bacillus. In a brief article on the uses of the fermentation tube published in 1890[3], I incidentally called attention to this difference as a valuable means of diagnosis. The fact, however, remained unnoticed and in 1891 Chantemesse and Widal[26] brought forth the same test as new, using lactose in place of glucose in the bouillon. Their method consisted in observing gas bubbles rising and forming a light froth on the surface of the culture fluid in ordinary flasks. This publication induced me to defend my priority in a second article in which I quoted the original announcement of the test[27]. But even this has been largely overlooked by subsequent writers.

The publication of Chantemesse and Widal first called general attention to the gas test as the older differential characters were melting away and something more definite was urgently needed in this very practical field. They were opposed at once by Dubief[28] who regarded the differences between these species as merely quantitative. Recently a number of writers (Tavel[29], G. W. Fuller[30], W. Dunbar[5], Germano and Maurea[31], Ferrati[32], and Pane[33],) have contributed long articles on this subject and all of them confirm the gas test and give it the most important place among the means of diagnosis between *B. typhosus* and the colon group. Dunbar in ignorance of my second article * naïvely recommends the bent tube, closed at one end, as the simplest means of determining gas production. The same thing had been suggested by G. W. Fuller in a prior publication as a substitute for the more expensive fermentation tube. Dunbar further recommends simple bouillon (*Fleischwasser*), a recommendation likely to lead astray as I have pointed out above. Since gas production in bouillon depends solely on the muscle glucose the test would fail when this is absent. The use of lactose, as suggested by Chantemesse and Widal is not so trustworthy as that of glucose, for we have a large group of pathogenic bacilli, the hog cholera group, easily confounded with *B. typhosus* because neither act on lactose and hence do not coagulate milk. The use of glucose bouillon would clear up the difficulty at once.

* This must have appeared before the conclusion of his work for he refers to a publication subsequent to mine.

The fundamental differences between *B. typhosus* and the colon group of bacteria need further elucidation by a thorough study of all the products of fermentation, as has been done by Dubief[28] and Peré,[1] but without concordant results as yet. For the typhoid bacillus likewise has a definite action on glucose, as has been shown by Brieger and recently by Peré. The latter has shown that when glucose is added to milk, it subsequently coagulates when inoculated by this organism. The action on glucose is moreover readily revealed by the markedly acid reaction of cultures in glucose bouillon. All that the gas test tells us definitely is that the colon bacteria act on glucose with evolution of a certain volume of gas, and that the typhoid bacillus acts upon glucose without the evolution of gas.

There is one question called up by the fermentation test which will require some attention. The evolution of gas with the simultaneous appearance of acids in the culture fluid might lead us to assume that at least some gas may have been set free from the Na_2CO_3 used to neutralize the bouillon. Yet by adding increasing quantities of sterile Na_2CO_3 solution to a series of fermentation tubes, I was unable to evolve any gas with the typhoid bacillus. It is not unlikely, however, that bacteria capable of setting free much acid may lead to the accumulation of a trifle of gas, not the product of fermentation, in strongly alkaline bouillon. In all cultures in which only small quantities of gas appear this possibility should be borne in mind.

THE QUANTITATIVE DETERMINATION OF FECAL BACTERIA IN WATER.*

The bacteriological examination of water in the interest of practical hygiene, has thus far suffered from the difficulty that the kinds of bacteria present are recognizable only when a disproportionate amount of labor is spent in isolating them. Occasionally bacteriological water analysis has taken a certain

* See the forthcoming Annual Report of the State Board of Health of New York for 1892, for a more detailed statement of this method.

definite direction, as in the search for typhoid bacilli and Asiatic cholera spirilla. For general purposes, however, the bacteriologist had to fall back upon the numerical estimation with no regard to any qualitative determination. The numerical estimate, taken by itself, is not satisfactory. It is true that in large surface waters, such as rivers, the number of bacteria is a very good index of the organic matter present, yet here one remains in doubt whether the bacteria are in the main from sewage or from decaying vegetable matter. Hence in the few instances in which I have had occasion to determine the hygienic character of a given water, I have endeavored to get some idea of the fecal bacteria present, in other words, the large group of colon bacteria which are such regular inhabitants of the intestines of man and of the domesticated animals and which are as good an index of sewage pollution as we can desire.

There are methods which enable us to isolate fecal bacteria from water, but they either do not give us any information concerning the number of such bacteria, or else this knoledge is obtainable only after much labor. Passing by these methods as not bearing on our subject, I will briefly refer to one which is an outgrowth of the observations on gas production in the fermentation tube.

If a series of such tubes containing glucose bouillon be inoculated, each with an equal but very small quantity of water and placed at once in the thermostat at 37° C., it will be noticed after one or more days, if the water is much polluted, that some contain gas. If, for example, one ccm. of water is distributed equally among ten tubes and of these, four subsequently contain gas, we may conclude that in one ccm. of this water there were four gas-producing bacteria. All gas-producing bacteria are not intestinal species, however. Hence we must try to eliminate those that are not fecal by the amount of gas present. Bringing together all the information obtained by cultivating a variety of bacteria in the fermentation tube, I have come to the conclusion that all tubes containing less than forty and more than seventy per cent. of gas are to be eliminated. The lowest limit drawn excludes *Proteus vulgaris*,

probably a putrefactive organism, pure and simple. The upper limit excludes *B. cloacæ*, which, in spite of its name, I cannot range among fecal bacteria. Between the limits of forty and seventy per cent. of gas are included all varieties of *B. coli*, the hog cholera group, *B. lactis aërogenes* and Friedländer's bacillus.

There are several objections which may be urged against this as against any approximative method. In the first place it does not include a large number of pathogenic species, among them *B. typhosus* and *Sp. choleræ Asiaticæ*. But, it may be answered, the object of the method is not to reveal all possible disease germs but to use the colon group as an index of pollution because, as I maintain, they must come directly from the digestive tract. The presence of *B. coli* even in small numbers is amply sufficient to make any water suspected.

In the second place it may be claimed that the evolution of gas may be either checked or augmented in the presence of a number of species in the same tube. This objection involves the rather broad subject of antagonism among bacteria, which cannot be discussed here. There are, however, a few facts which show the objection to be in the main pointless. In the thermostat only very few bacteria from water develop owing to the high temperature, so that rarely more than one species survive and multiply in the fermentation tube if the quantity of water added be not too great. Again, the presence of two gas-producing bacteria in the same tube is not likely to occur owing to their relative scarcity. To test their mutual behavior, however, I inoculated a number of tubes simultaneously with two different gas-producing species. In general *B. coli* produced the quantity of gas peculiar to it, unless *B. cloacæ* was inoculated with it. In one out of three trials *B. cloacæ* triumphed and drove out all fluid from the closed branch, in the other two *B. coli* conquered. There may, therefore, be an occasional masking of the presence of *B. coli* by *B. cloacæ*. This error will not occur if small quantities of water be used or if the experiment be repeated in the event that more than half the tubes inoculated show gas production.

The concurrence of the many aërobic bacteria with the colon group in the fermentation tube even if they should be able to multiply at the temperature of the thermostat is made negative by the fact that the former are unable to multiply at all in the closed branch.

WASHINGTON, D. C.,
July 28, 1893.

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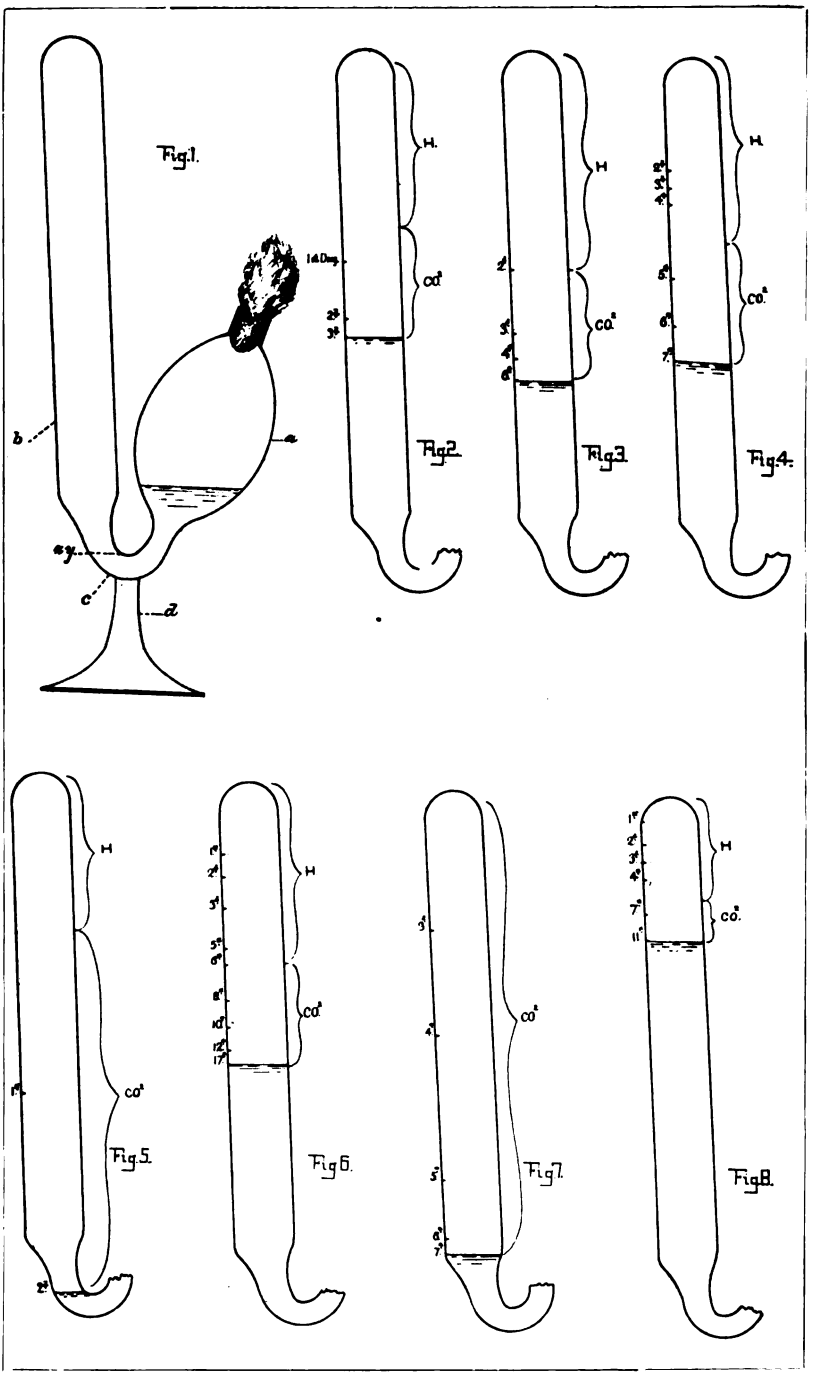


FERMENTATION TUBES—THEOBALD SMITH.

DESCRIPTION OF PLATE.

(All figures reduced one-half.)

Fig. 1. The fermentation tube as used in the foregoing investigations. *a*, The bulb freely exposed to the air filtering through the cotton wool plug; *b*, the closed branch; *c*, the connecting tube; *d*, the foot. The tube used in the foregoing investigations requires about 25 cc. of bouillon, 20 of which belong to the closed branch. The line *xy* divides the aërobic from the anaërobic portion of the tube. This line is very sharply drawn by aërobic bacteria. The turbidity on the one side bounds absolute clearness on the other. In facultative anaërobic cultures there exists at this line a sudden marked change from turbidity to mere cloudiness.

Fig. 2–8. Graphic representation of gas production by different bacteria in different sugar solutions. The short lines on the left margin of the tube show the rapidity with which gas accumulates and serve as a means of comparing different types. The volume of CO_2 and H found at the close of the period of gas production is indicated by brackets on the right margin of the tube.

Fig. 2. *B. coli communis* in glucose bouillon.

Fig. 3. The same bacillus in lactose bouillon.

Fig. 4. The same bacillus in saccharose bouillon.

Fig. 5. *B. cloacæ* in glucose or saccharose bouillon.

Fig. 6. *B. cloacæ* in lactose bouillon.

Fig. 7. *Saccharomyces cerevisiæ* (isolated from compressed yeast) in glucose or saccharose bouillon.

Fig. 8. *B. coli* in peptone bouillon. The gas formed indicates the presence of considerable muscle glucose.

MUSCULAR ATROPHY CONSIDERED AS A SYMPTOM.

By WILLIAM CHRISTOPHER KRAUSS.

Atrophy, or wasting of the muscular fibers, whether occurring insidiously or *en masse* may or may not be indicative of disease of the nerve centers. Although not of such serious import that its recognition demands early therapeutic procedures, nevertheless, it is necessary to detect the cause of this retrogression in order to render a correct prognosis and to plan the proper treatment. Diseases of the brain and spinal cord are, as a rule, sub-acute or chronic, run a long course, manifest themselves by vague, indifferent symptoms and yield grudgingly to the resources at the neurologist's command. Wasting of the muscles is one of the most prominent of the objective symptoms of brain and cord disease, and if properly considered and appreciated may give us important clues for the location and detection of the neural lesion with which we are confronted. It is by no means pathognomonic, but when associated with other groupings of subjective and objective symptoms, becomes at once characteristic of definite lesions in the brain, cord, peripheral nerves or muscle itself.

The premise must not be inferred, however, that all muscle degeneration is pathological or dependent upon some initial lesion in the nerve centers, for it is a fact that wasting of muscles occurs independently of any nerve or muscle lesion, but is due to purely physiological changes, or the active cell growth is no longer predominant, and has been succeeded by a period of involution or cell decay. This we call senile wasting or acute atrophy. Another form of atrophy, or lack of development, which must not be confounded with either physiological or pathological wasting, is aplasia and hypoplasia of the extremities, conditions arising in utero due to the arrested development of the embryo as a whole or in part. These developmental

defects are the result probably of some constriction or pressure from folds or bands of the fœtal membranes, or by loops of the umbilical cord. Cases of this kind are by no means rare but have been carefully studied by Fœrster, Voight, Gruber and others. The different classes are distinguished according to the degree of malformation as follows:

(1) Amelus. Limbs entirely wanting or replaced by wart-like stumps.

(2) Peromelus. All four extremities stunted.

(3) Phocomelus. Limbs consisting merely of hands and feet sessile upon the shoulders and pelvis.

(4) Micromelus. Limbs regular in form but abnormally small.

(5) Abrachius and Apus. Absence of upper limbs, while the lower are well formed, and *vice versa*.

(6) Perobrachius and Peropus. Arms and thighs normal; forearms and hands, legs and feet malformed.

(7) Monobrachius and Monopus. Absence of a single upper or lower limb.

(8) Sympus apus and Sympus opus. Absence of feet; or they may be represented by single toes, or by one foot as in siren monsters.

(9) Achirus and Perochirus. Absence or stunted growth of the entire hand or foot. (Ziegler.)

It is not the purpose of this paper to invade the field of teratology, but to study another morbid process which also ends in defect of structure, not, however, through interference of growth, but through the destruction and degeneration of muscles once able to perform work measured by their development and vitality. This process is more properly termed regression or retrogression, and the designation muscular atrophy as commonly employed has reference only to a retrograde metamorphosis of a fully developed muscle.

Inasmuch as there are atrophies due to physiological and also others due to pathological processes it is of the utmost importance to distinguish between them. Generally speaking, physiological atrophy occurs as the result of the decadence of the vital powers due to senile changes. It is not attribut-

able to any direct appreciable lesion and the atrophy is considered as active. Another class, bordering closely upon physiological atrophies, is caused by derangements in whole or in part of the constructive organs, febrile processes, etc. These latter are considered as passive, and the atrophy is unlimited in its extent. Local atrophies, due to mechanical hindrances, injury to the tissues, through interference of the circulation, and overwork are also examples of passive atrophies.

Pathological atrophies on the other hand, are the results of demonstrable organic lesions either in the brain, cord, peripheral nerves or muscles, follow certain laws in their distribution, and are accompanied by subjective and objective symptoms characteristic of the focal lesion.

Subjective signs. — The advent of progressive muscular atrophy in many cases, and especially in those other forms of atrophy not dependent upon acute inflammatory processes, is ushered in by some localized, deep-seated, aching pain, to which little attention is paid. In others, some slight sensory disturbance, as a feeling of numbness, heaviness or sharp lancinating pains as in neuritis, may precede the atrophy, while in many no warning whatever is given of the enfeeblement which is soon to occur. Generally, the first thing that attracts the patient's attention is the inability to execute certain movements, which, but a short time ago, he was able to carry out with ease and dexterity. If he be an artisan, and the atrophy begins in the muscles of the hand, as it so often does, the weakness will soon incapacitate him for his work ; if a laborer and the atrophy first affects the shoulder muscles, or muscles of the back, or if a pedestrian and the peroneal muscles succumb early, he is soon made cognizant of some loss of power, which to him remains for some time unaccountable. This weakness is often ascribed to overwork, exhaustion or fatigue, and the usual remedy—rest—fails to restore to the former condition. I have met patients in clinics, especially females, in whom atrophy of the muscles of the hand and arm had existed for years, and attention was first called to it by the physician while examining for some other ailment. Instruments have been devised for measuring approximately the strength of the

arm and leg muscles, and although the figures may vary somewhat at each trial, still they are accurate enough to indicate the progress of the wasting. The dynamometer is perhaps the best instrument for estimating the power of the flexors of the fingers and hand muscles. It consists of an oval steel spring with a dial and index in the center. Compression of the spring is indicated on the dial in pounds and kilograms. This instrument is by no means accurate or perfect as each succeeding trial may give a different reading according to the strength exerted by the patient. It is my practice to take the average of two or three compressions and this result I consider approximately correct.

FIG. 1.

For estimating the strength of the legs several appliances have been suggested by Dana, Birdsall, Fèrè, and d'Onimus, but none have enjoyed universal adaptation among neurologists. An apparatus which I have recently described* approaches, in my opinion, the solution of this problem, and has received the appellation, *Pedo-dynamometer.* It consists of a wide, heavy belt (*a*), its inner surface padded so that its adjustment around the waist will not be uncomfortable. A heavy webbing (*b*), is looped through the belt passing over the shoulders, which helps to retain the belt in its proper position. A common Mathieu dynamometer (*c*), is connected with the belt (*a*), by means of a strong adjustable strap, permitting it to be lengthened or shortened according to the stature of the patient. Connected to the dynamometer (*c*), is a stirrup (*d*), the base of which is padded for receiving the foot. Pressure exerted

*Neurologisches Centralblatt, June 1, 1893.

upon the stirrup will be registered upon the dial of the dynamometer and the approximate strength of the extensors of the leg can be ascertained. By lengthening the strap which connects the dynamometer with the belt (*a*), and flexing the foot on the leg as much as possible then allowing the patient to push, the power of the extensors of the foot can be also determined. In applying the Pedo-dynamometer, the thigh should be flexed upon the pelvis to an angle of 135 degrees, the leg flexed upon the thigh to an angle of 90 degrees at the knee. It may be adjusted in the standing or recumbent position. By using snaps the dynamometer can be quickly removed and used to measure the power of the hands.

In advanced cases the patient is very susceptible to changes of temperature, particularly from warm to cold, and in winter the atrophied members must be heavily padded to insure comfort. In those cases where rheumatic pains have preceded the atrophy, and also in those cases of neuritic and spinal origin, there is some loss of sensation and other disturbances, but in the great majority of cases the general sensibility is unimpaired.

As a rule, pain is absent in muscular wasting except in cases of neuritic and spinal origin, and here the pain is a neural pain and not a muscle pain. Pressure over the course of the inflamed nerves or on the spine will call forth sharp, shooting pains, whereas pressure applied to the muscle will elicit no complaint.

The objective signs offer the physician an important and interesting field for study and observation. His attention, as was that of his patient, is directed at once to the wasting or atrophy of the different muscles. The natural effect of this is to rob those portions of the body of their normal contour and beauty, and bring into prominence the underlying hard structures. This wasting may be limited to a single muscle, to a group or system of muscles, may be unilateral or bilateral, general or localized, according to the cause and seat of the primary lesion. In estimating the extent of the atrophy, some more definite means are necessary than merely the sight or touch—and the tape measure is called into service.

A tape measure which seems to answer every purpose and which has been cordially received by many neurologists, was described by me in the Journal of Nervous and Mental Diseases, 1890, page 128. It consists of a tape (1) one meter long and one centimeter wide. The English scale is graduated on one side and the metric scale on the other. The head is supplied with a swivel (3), through which passes the free end of the tape, permitting of uniform tension, greater accuracy in reading, and of its being held with one hand.

The second tape (2) is one-half meter long and one-half centimeter wide, and is provided with a sliding head, through which the first tape passes. This tape is, therefore, at right angles to, and movable upon, the first tape. It is also graduated after the English and metric scales. The object of this tape is to ascertain at what distance from a certain fixed, bony point the first tape has been applied, so that on succeeding occasions the measurement may be taken at the same point. To illustrate: If the tape (1) be applied to the arm at a distance of seven and one-half centimeters from the internal condyle of the humerus (reckoned by means of tape 2), it is obvious that on succeeding occasions, or in comparison of the two extremities, the tape (1) must be applied at exactly the same point, thus excluding all possible chance of error.

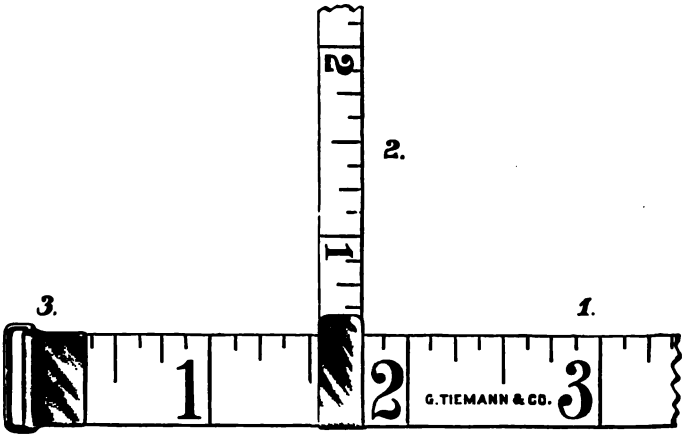


FIG. 2.

My manner of using the tape is as follows: For the upper arm, I select the internal condyle of the humerus as the fixed point. Then measure off seven and one-half centimeters with tape No. 2. At this point the circumference of the arm is taken by means of tape No. 1. In like manner the circumference of the arm is noted at distances of fifteen, and twenty-two and one-half centimeters from the fixed point. For the lower arm exactly the same procedure is followed beginning at the proximal end and taking the circumference at seven and one-half, fifteen, and twenty-two and one-half centimeters from the internal condyle. For the hand a distance of ten centimeters is measured from the tip of the middle finger and the circumference taken at this point.

For measuring the circumference of the leg, I employ the internal condyle of the femur as the fixed point and take measurements at seven and one-half, fifteen, twenty-two and one-half, and thirty centimeters respectively from the internal condyle. In taking the circumference of the abdomen or thorax I choose the umbilicus as the fixed point.

The atrophy of muscular fibers and the hyperplasia of the connective tissue lead to contraction of the latter, and permanent contractions and distortions of the body and extremities result; the same is produced if a system of muscles becomes affected and the opponents, remaining intact, predominate. The peculiar shape of the hand in the Duchenne-Aran type, sometimes called "main en griffe," the "turkey gait" in the myopathic forms, etc., are examples of this kind.

The integument of the atrophied members has a shrivelled, purplish appearance, and the finger nails lose their pinkish tint. Other trophic disturbances, except in atrophies due to a neuritis, are wanting.

In many cases a fibrillary contraction, wave-like in appearance, propogated in the direction of the fibers may be observed occurring either spontaneously or by gently tapping the muscle. This fibrillation, as it is termed, is of short duration, returns after an interval of a few seconds, may be limited to a muscle, or part of a muscle, or may extend over the whole of the affected part or member. It is not pathog-

nomonic of progressive muscular atrophy, as was formerly supposed, but has been observed in other affections of the muscular system, and even in the healthy muscle.

Loss of Myotatic Irritability. Tapping a healthy muscle produces a slight contraction of the fibers, which calls forth the performance of its function. In the diseased muscle the reflex arc is broken, the centripetal-sensory path remaining undisturbed, while the centrifugal-motor path is broken. The loss of tendon reflexes, in some forms, occurs quite early, even before any serious damage has taken place in the muscular fibers. The patellar and elbow reflexes are the ones most generally tested.*

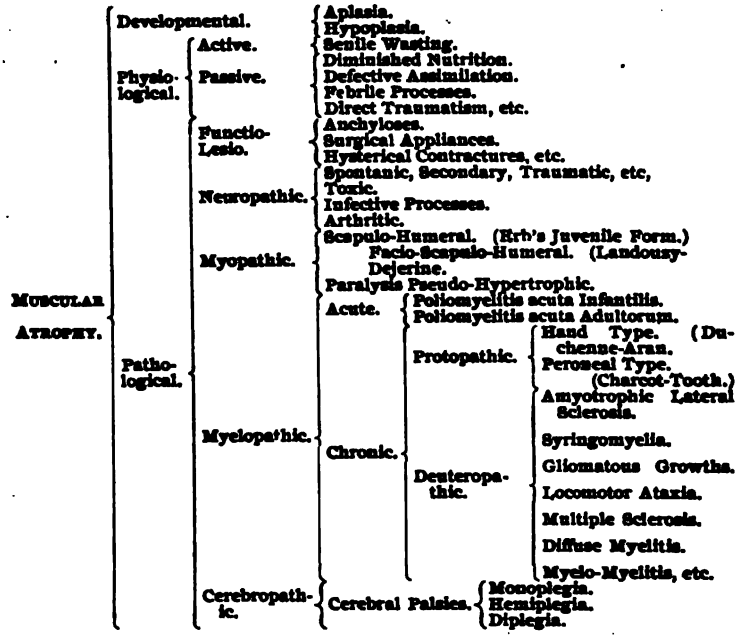
Electrical Irritability.—To Duchenne (de Boulogne) must be given the credit of having first employed electricity as a diagnostic and therapeutic agent. His method of localizing the electrical current, published in 1850, has served as the foundation for all later electrical researches in medicine. The elder Remak appeared against him, disputing some of his conclusions, particularly as to whether the contraction of the muscle was produced by irritating the bulk of the muscle, or the entrance of the motor nerve into the muscle. Von Ziemssen, taking advantage of this breach, made experiments upon dying patients, and, by careful dissection afterward, discovered that the motor points were those points where the motor nerve approached nearest the surface (1857). The natural law of muscular contraction under the influence of the galvanic or faradic current, shows the superiority of the cathode over the anode, the contractions being short, sharp and quick. The wasted muscle presents changes of electrical irritability dependent upon the degree and extent of the degeneration. Erb and V. Ziemssen conducted a series of experiments upon diseased muscles, and arrived at practically the same conclusions at exactly the same time—1868.

Their law, called the *Entartungs Reaction*, reaction of degeneration, is as follows: First degree, or partial reaction;

* See author's paper on Tendon Reflexes, Buffalo Medical and Surgical Journal, December, 1892.

faradic and galvanic nerve irritability preserved, but weakened; faradic and galvanic muscle irritability preserved, but the contractions, instead of being short, sharp and quick, are slow and vermiform. In the second degree, or complete degenerative reaction, the galvanic and faradic nerve irritability and faradic muscle irritability are lost, but the galvanic muscle irritability is increased. The action of the poles is, however, reversed, the anode closure contraction being greater than the cathode closure, and thirdly, the contractions are slow and vermiform. In the third degree, or severe type, there is entire loss of galvanic and faradic nerve and muscle irritability. Any one of these three degrees may be present, according to the seat and character of the primary lesion. Of these symptoms, the wasting and weakness are the only ones which are truly pathognomonic. The others, which are characteristic, are present in some forms of muscular atrophy, and absent in others.

Diagnosis.—To diagnose a case correctly, two essentials are necessary: First, a thorough knowledge of the symptoms, and second, a good working classification in which each particular variety has its only and proper place. One of the best lessons taught us by our esteemed teacher whom we delight to honor to-day, was to properly classify and arrange all facts so that they could be most readily consulted. If this is good practice in the scientific laboratory, it certainly must apply to the human laboratory with even greater force. The study of the tumors was vague and unscientific until Virchow proposed his peerless classification. Charcot's classification of the different forms and symptoms of hysteria has brought order out of chaos, and the study of hysterical affections is to-day more advanced and scientific than many of the longer recognized diseases. Therefore, I hold that to be able to diagnose correctly the different forms of muscular atrophy, symptomatically considered, one must have at command a classification based upon the underlying pathology. A classification which has served me well, was described by me in the *Buffalo Medical and Surgical Journal* for April, 1891, and is here appended, with but one or two slight changes.



The different forms of developmental defects have been sufficiently considered in another part of this paper. Under the head of physiological atrophies are placed two forms, the active and the passive. With the active atrophy is classed senile wasting or the retrogression of old age. This form is more or less general, affects all organs and tissues and has but one termination, the result of all decay—death.

Belonging to the passive atrophies, or those processes which are the result of disorders of the constructive organs may be mentioned the wasting of the tissues following diminished nutrition, defective assimilation, febrile processes, constitutional diseases, malignant growths, etc. The atrophy is general, attacks no particular group of muscles, tissue waste is greater than tissue repair, and the atrophy continues until a reaction sets in when the primary affection either goes on to recovery or to a fatal termination. The diagnosis of this group is simply the diagnosis of the fundamental disease. No

attempt need be made to treat the functional atrophies *per se*, as in the great majority of cases they are passive, dependent upon disorders of the system, which when relieved permit the atrophies to disappear.

Pathological atrophies are either atrophy of inaction, (functio lesio) or tropho-neurotic. The former can hardly be classed as pathological, less physiological. They result when the functional activity of the cells is interfered with, and the nutritive changes are therefore diminished or abolished. As a result the member grows smaller and weaker and continues so until the cells regain their normal activity. Under this head we meet atrophies due to anchyloses, surgical appliances, hysterical contractures, etc. I have seen the arm reduced to skin and bone in cases of hysterical contracture, and, although the rest of the body was well nourished and developed, still the unused extremity was in a state of extreme atrophy. It is a simple matter to diagnose such muscular wasting because it is local, the cause is so very apparent and symptoms pointing to complication are generally absent. No pathological lesion can be found except a diminution in the bulk of the muscle fibers. The treatment of these cases is very satisfactory.

The tropho-neurotic atrophies are pathological and their causes may be sought for in some disturbance along the course of the peripheral nerves, spinal cord, brain or muscles. These atrophies have a distinct and clearly definable pathology, and are accompanied by symptoms indicative of an organic lesion permitting of accurate diagnosis.

Neuropathic Atrophies. — Inflammatory conditions of the peripheral nerves are productive of muscular wasting along the course of the nerves. This class of atrophies may be termed neuritic or neuropathic. If the atrophy follows a neuritis, as in acute simple neuritis, multiple neuritis, endemic neuritis, hemiatrophia-facialis, or a neuritis consequent to trauma, pressure, chemical or thermal irritation, or secondary to some inflammation of a neighboring organ, it is always accompanied by the general symptoms characteristic of nerve inflammation.

Toxic Atrophies. Agents which have been instrumental in setting up a neuritic process and a consequent wasting of the muscles are—alcohol, lead, arsenic, mercury and bisulphide of carbon. The atrophy is generally limited to the extensor muscles, as seen in alcoholic paralysis, lead palsy, arsenical pseudo-tabes, and on eliminating the poison from the system, the atrophy sometimes disappears.

After Infective Processes. Following upon an acute attack of diphtheria, variola, typhoid, typhus, cerebro-spinal meningitis, etc., atrophic changes may take place in some of the muscles of the body. The lesion is generally neuritic, the atrophy either the simple or hyaline degenerative, the latter especially in typhoid, variola and cerebro-spinal meningitis. In typhoid fever, typical hyaline degeneration of the rectus abdominis and adductors of the thigh may frequently be met with.

Arthritic Atrophies. Following injury to joints, atrophy of the muscles moving that joint, but more especially the extensors, is often observed. If the hip joint is the seat of injury, there is atrophy of the glutei ; if the knee, the rectus femoris ; if the ankle, the gastrocnemius and soleus. The wasting is quite often pronounced and persistent, with little, if any change in the electrical irritability, and increased tendon reflexes. The seat of the lesion is purely hypothetical. Vulpian, Charcot and others believe that the articular centripetal nerves convey the irritation to the gray matter and particularly to the motor cells of the ventral cornua, thence to the muscles of the joint through the efferent nerves.

The diagnosis of these neuritic atrophies is not difficult inasmuch as they are always accompanied by pain over the course of the nerves, trophic and vasomotor disturbances. The wasting is local, limited, generally of a severe type with marked electrical reactions, and, being dependent upon a neuritic process, generally subsides upon cessation of the inflammation.

Of late there seems to be a disposition to classify another form of muscular atrophy under this head, namely, the peroneal type, commonly called the Charcot-Tooth type. Erb and

Hoffman have recently published cases in which neuritic symptoms were present, such as sensory disturbances, marked electrical reactions, local distribution, appearance after infectious diseases, etc. Hoffman believes that this neuritis is secondary to changes in the ventral cornua. If this is really the case I see no reason why this type of atrophy should not be considered under the myelopathic forms. Sachs who has studied this form of atrophy very thoroughly, is disinclined to accept Hoffman's ideas as to its pathology and relegates it to the spinal form of muscular atrophy.

The primary lesion in these neuropathic forms is to be sought for in the nerves supplying the affected muscles. The neuritis may be either interstitial, parenchymatous or degenerative. In the interstitial form the medullary sheath is broken into fine granules of fat and debris and absorbed. The axis cylinder is swollen, degenerated, and may be likewise absorbed. The nuclei of the sheath of Schwann become swollen and proliferate, leading to the formation of new connective tissue, which, after the period of regeneration, consti-

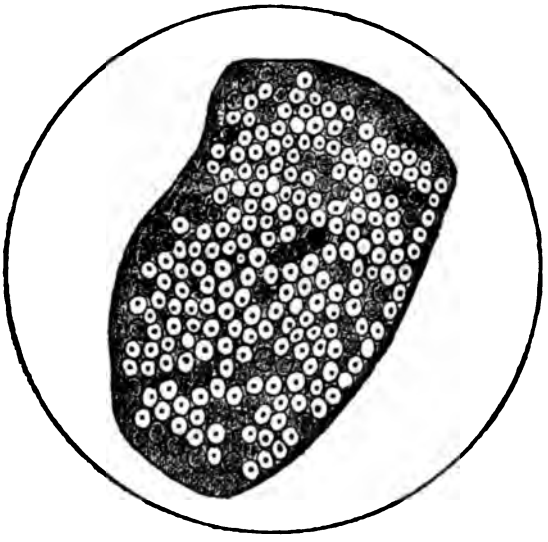


Fig. 3.

tutes the bulk of the nerve fiber. The perineurium and endoneurium also take part in this process and become converted into thick layers of connective tissue.

The neuritic processes following the infectious diseases, especially diphtheria, afford good examples of the parenchymatous form of neuritis. Fig. 3 shows the oculo-motorius nerve in a case of diphtheria, the seat of marked degenerative changes.* Many of the axis cylinders have disappeared, while others are smaller and have lost their sharpness of contour. The white substance of Schwann has absorbed the staining fluid indicating some changes in regard to chemical composition.

In discussing the various forms of muscular atrophy, we have only described diseases and conditions in which wasting of the muscles was a prominent symptom not by any means characteristic or pathognomonic. Other symptoms were always present which denoted more forcibly than the atrophy the seat of the disease or cause of the wasting. In the following types the atrophy of the muscles is the predominant sign, so much so that these affections have been designated progressive muscular atrophy and progressive muscular dystrophy.

Myopathic Atrophies.—The myopathic forms of muscular atrophy are universally designated as progressive muscular dystrophy, after the recommendation of Erb of Heidelberg. They include several analogous types clinically and perhaps pathologically, although the focal lesion has not been ultimately determined. They develop in the young, are relatively rare and as yet the exact pathology is undetermined. Erb is of the opinion, recently expressed, that there may be some slight changes in the ventral cornua as yet undiscovered, and that the myositis or lipomatosis is really secondary to organic changes in the nervous system.

Erb's juvenile form is the most prominent type of the

* See Author's paper on Diphtheritic Paralysis in Neurologisches Centralblatt, No. 17, 1888.

myopathic forms of muscular atrophy. It usually begins in the muscles about the shoulder girdle, upper arm and back. The pectoralis major and minor, biceps, brachialis anticus, supinator longus, serratus magnus, rhomboidei, trapezius, sacrolumbalis, latissimus dorsi and longissimus dorsi are the muscles most often atrophied. The sterno-cleido mastoid, levator anguli scapulae, coracobrachialis, teres, deltoid, supra and infraspinati, rectus abdominis and the small muscles of the hand remain undisturbed. The muscles of the lower extremities which are at times affected are the glutei, the quadriceps, the adductors, the peronei and the tibialis anticus. The sartorius, gastrocnemius and soleus remain as a rule unaffected. Occasionally hypertrophy of some of the muscles is observed, notably the deltoid, infraspinati, triceps, tensor fascii and muscles of the calf.

This type of atrophy affects several members of the same family, appears generally before the twentieth year, and has a decided preference for females. It is not accompanied by fibrillary twitchings, reaction of degeneration is not present, and the tendon reflexes are unimpaired.

Analogous to this type is the facio-scapulo-humeral type, first described by Duchenne as the forme héréditaire; but later more fuller and minutely by Landouzy and Dejerine, in 1885. The wasting of some of the muscles of the face and hypertrophy of the lips gives a peculiar tapir-mouth appearance to the patient, "facies myopathique." With this exception, this type of atrophy corresponds exactly with Erb's form, and is regarded by many as one and the same.

Another form is the pseudo-hypertrophic paralysis of Duchenne. Although hinted at years before by Bell, Meryon, Oppenheimer and Partridge, it remained for Duchenne, in 1861, to interpret correctly its clinical importance and establish it firmly in our nosology. It is no doubt hereditary, and occurs more frequently in boys than in girls. The important symptoms are weakness in the muscles of the leg and back, a waddling gait, an apparent increase in the size of the muscles of the calf, and sometimes of the thigh and calf. Furthermore, there is lumbar lordosis brought about by wasting of the muscles of

the back and extensors of the thigh, some contractures, and a peculiar difficulty in rising from the ground. Repeated examinations of the nerves and cord have been unsuccessful, and hence the inference that the muscle itself is the seat of the lesion, although the notion is gaining ground that the real lesion may be located in the nerve centers, perhaps in the spinal cord.

To understand better the pathological changes occurring in the muscles, it may be desirable to review briefly the histology of a muscular fiber. A striated muscle is composed of a number of bundles, surrounded by a layer of areolar tissue, the external perimysium. Each bundle or fasiculus, enveloped by a thin, delicate membrane, the internal perimysium, is composed of bundles of fibres, separated from each other by a delicate connective tissue, the endomysium. These fibers are arranged parallel to each other, are from two to four centimeters in length, and are united either to the tendons or aponeuroses, or else connected with the adjacent fibers.

Each fiber is composed of a number of filaments or fibrillæ, inclosed in a transparent homogenous membrane, designated by Bowman, the sarcolemma. In the mammalia, elongated nuclei are present on the internal surface of this membrane. The primitive fibers are cylindrical or prismatic in form, about sixty-five microns in breadth, and their length depends not so much on the length of the muscle, as upon the arrangement of the tendons. They are marked by transverse and longitudinal lines or striæ, giving them a characteristic, striated or striped appearance. I will not take up the histology of the primitive fibrillæ, but will limit myself to the primitive fiber. (See Plate, fig. 1).

Each fiber has a vascular and nervous supply, the former being furnished by the ramifications of the capillaries, running parallel between the fibers. The nervous supply is from the moter nerves, and their termination in the muscle has been the subject of much controversy. The motorial endplates of Kühne or nerve hillocks of Doyére are generally recognized by most recent observers. The nerve terminates below the sarcolemma, where the medullary sheath becomes

blended with it, forming a plate or plaque which is raised somewhat from the fibers, but never encircles it. The axis cylinder is distributed to this plaque, but does not penetrate the interior of the fiber. The origin of the efferent or sensory nerve fibers in the muscle is still a matter of uncertainty.

Fatty infiltration and degeneration of the muscular fiber, as occurring in the myopathic form of atrophy has been designated as myositis or lipomatosis. Here hyperplasia of the interstitial connective tissue and fatty infiltration follow closely upon the wasting of the muscle, and cause either no apparent change or else a slight increase in its volume. The muscle appears pale, yellowish, has a greasy feel, and resembles closely, not only macroscopically, but also microscopically, a lipoma, or, better, a myo-lipoma. Under the microscope, the large, round, yellowish cells, with dark borders, make up the greater portion of the tissue. Here and there a muscular fiber, with its transverse and longitudinal striation still intact may be observed. (See Plate, fig. 3.)

The interstitial connective tissue is much increased in volume, with proliferation of its nuclei. The substitution of fat may be so pronounced as to give the muscle an hypertrophied appearance, and hence the denomination pseudo-hypertrophy, given this affection by Duchenne in 1861. In some forms of dystrophia, the muscular fiber may be even increased in volume, giving rise to real hypertrophy, a condition sometimes met with in idiopathic muscular atrophy.

Myelopathic Atrophies, or Atrophies dependent upon Lesions in the Spinal Cord.—They may be acute or chronic. The acute forms are poliomyelitis acuta infantilis (infantile paralysis) and poliomyelitis acuta adultorum. Although not conclusively proven, still it is generally supposed that the onset of this type of inflammation is due to some infection. Cases are very common, both in the infantile and adult forms, where an infectious disease preceded the attack. I have reported a case occurring in a man forty-three years of age where the poliomyelitis was undoubtedly the result of measles.

The acute stage is ushered in by general malaise, headaches, pains in the back and limbs, fever, rapid pulse, somnolence,

delirum, convulsions, and in a short space of time a general or partial paralysis sets in. After the decadence of the acute stage, the paralysis confines itself to one, rarely several, of the extremities. The muscles waste rapidly and show degenerative electrical reactions, the tendon reflexes are absent, trophic changes are present, but no disorder of sensation. If one of the legs be affected, the gait becomes very characteristic owing to the atrophy and weakening of the peroneal muscles. The patient is obliged to throw the foot far forward, the toes striking the ground first. Charcot calls these patients "steppeurs."

In the adult form the disease is not so liable to recede and the affected members remain often permanently powerless.

The chronic forms comprise most of the chronic affections of the cord. They are divided by Charcot, according to the seat of the lesion, into protopathic, where the lesions are solely and alone in the gray matter; and deuteropathic, where the gray matter is only secondarily affected. Under the first head we have the Duchenne-Aran, or hand type, characterized by wasting beginning in the small muscles of the hand, as the interossei, superficial and deep muscles of the thenar and hypothenar, then extending to the flexors and extensors of the fingers, biceps, brachialis anticus, supinator longus, pectoralis major, trapezius, infraspinatus, supraspinatus, rhomboid, serratus magnus, latissimus dorsi and sometimes, though rarely, the flexors and extensors of the hip. The tendon reflexes are absent, fibrillary twitchings and altered electrical reactions are present There are no symptoms indicative of trophic changes or disorders of sensation. This type of atrophy is the original form of progressive muscular atrophy described by Duchenne and Aran in 1848 and 1850.

In 1886 there appeared simultaneously from Charcot and Marie in France, and Tooth in England, the description of another form of atrophy. Its mode of onset is by attacking the muscles of the lower extremities, the extensors of the toes and the small muscles of the feet. As a result there develops a double club foot which is quite characteristic of this type. The peronei, the calf muscles and later on the muscles of the

thigh become affected. The muscles of the hand and forearm may become involved after a lapse of years, producing the peculiar "main en griffe" so characteristic of the Duchenne-Aran type. This form of atrophy begins as a rule in early life, is a family disease, attacks and progresses uniformly on both sides, produces a double club foot, is attended at times with slight disturbances of sensation and vasomotor changes, and retains the tendon reflexes to a late stage.

The pathology of these forms has been the subject of long and earnest controversy. The peripheral or myopathic origin was stubbornly held by Friedreich and the German school, while Cruveilhier, Charcot, Lockhart Clarke and others clung to the central or spinal origin theory. The latter is now the one universally accepted.

The ventral cornua of gray matter present the results of a subacute inflammatory process leading to complete or partial destruction of the ganglion cells, sclerotic changes in the neuroglia, blood-vessel changes, cell proliferation, etc. The contraction of the newly formed connective tissue may even lead to the formation of cavities in the gray matter. (See Plate, fig. 4.) The ventral spinal roots are affected secondarily, likewise some of the efferent nerve fibres. Charcot's theory, then, is as follows: Atrophy of the muscular fibers is the direct result of irritation, which, beginning in the ganglion cells of the ventral cornua, is propagated through the ventral spinal roots and efferent nerves to the muscular fiber. Friedreich's theory was that the primary insult was a myositis with secondary changes as ascending neuritis of the peripheral nerve trunks, which terminated in a chronic myelitis.

The pathology of the Charcot-Tooth or peroneal type is still *sub judice*. Hoffman of Heidelberg has studied this form very carefully and has declared it to be of neuritic origin. He, therefore, has proposed to designate it "*progressive neurotic muscular atrophy*." Other observers still cling to the spinal theory, and until definitely proven by careful microscopical examination that it is primarily a disease of the peripheral nerves it may be classed among the atrophies of spinal origin.

I have under observation a case of this type of atrophy in

which all the symptoms point to disease of the ventral cornua of the spinal cord. Sensory disturbances and vasomotor troubles, symptoms of neuritic processes, are entirely wanting.

The pathological changes found in the atrophied muscles in the myelopathic forms correspond to simple degenerative atrophy. To the naked eye there is little to be seen save the diminution in size, and the pale, pinkish hue of the fibers; to the touch, a soft, spongy feel, with occasional cord-like prominences, instead of a firm, resistant mass. The entire muscle, if carefully removed, will be found shorter than normal owing to the contraction of the interstitial connective tissue. Under the microscope the condition is as follows: If the atrophy is not too far advanced, the fibers retain their normal appearance—transverse and longitudinal striation—but are somewhat narrower. As the process advances, the fibers split up into longitudinal fibrillæ, or transversely into discoid masses and then gradually disappear. In other cases fatty and vitreous degeneration may occur, and the fiber then has the appearance of a sheath containing a clear material with some fat globules. The intensity of this process is not the same throughout the muscle, patches of healthy fibers may be found surrounded by others in different stages of atrophy. Proliferative changes occur in the nuclei of the muscular fibers, and may lead to a new cell growth within the sarcolemma, replacing the contractile substance. Proliferation of the interstitial tissue also occurs and to such an extent as to separate the neighboring fibers. The entire muscle may, in fact, be converted into bands of connective tissue with some fat globules interposed between the separate layers. (See Plate, fig. 2.)

The true designation of muscular atrophy considered as a *morbid entity* applies only to those affections in which progressive wasting of the muscles is the reigning symptom. As such Erb's juvenile form may be taken as a type of those atrophies in which no focal lesion has as yet been discovered in the nerve centers, but the muscle has been regarded as the seat of the disease. As varieties, or deviations, may be mentioned the facio-scapulo-humeral type of Landouzy and Dejerine, and the pseudo-hypertrophic paralysis of Duchenne.

Secondly, those forms of myopathy due to a chronic anterior poliomyelitis such as the Duchenne-Aran or hand type and perhaps the Charcot-Tooth or peroneal type.

The deuteropathic form comprises those affections in which the involvement of the gray matter of the cord is secondary. The atrophy following may be quite pronounced as in amyotrophic lateral sclerosis, syringomyelia, and bulbar paralysis. A careful examination is necessary at times to distinguish between the atrophy of these affections and progressive muscular atrophy ; especially is this true of amyotrophic lateral sclerosis and syringomyelia. These affections stand in close relation to progressive muscular atrophy clinically and pathologically ; nevertheless they can be diagnosed by symptoms which are more or less pathognomonic. In amyotrophic lateral sclerosis the atrophy affects the muscles of the hand, arm, shoulder and back simulating closely the Duchenne-Aran type of muscular atrophy. In exceptional cases the lower limbs become implicated. Contractures develop especially in the terminal stage. The tendon reflexes are markedly exaggerated, locomotion is difficult and, what is very characteristic, the disease runs its course in two to three years. In regard to the duration and course of progressive muscular atrophy and amyotrophic lateral sclerosis there is difference enough to convince any observer that the two affections are distinct from each other. In regard to syringomyelia, although the atrophy resembles the distribution in the Duchenne-Aran type, still it is not so uniformly advanced on both sides, and the sensory and trophic disturbances which are always present enable one to make a differential diagnosis. In bulbar paralysis the focal lesion is of the same general character as in progressive muscular atrophy, but limited to the ganglion cells in the medulla and pons. Atrophy of the parts innervated by the cranial nerves will be the result ; in rare cases this process may extend caudad affecting the ganglia of the spinal nerves.

In locomotor ataxia, multiple sclerosis, neoplasms of the cord, diffuse myelitis and myelo-myelitis, the atrophy is less pronounced, inconstant, and variable in its seat and intensity.

Lastly, cerebropathic atrophies, generally observed in the

spastic paralysis of children and adults. The atrophy is limited to the paralyzed members, as in monoplegia, hemiplegia and diplegia. In the majority of these cases the atrophy is slight, due more to the inactivity of the paralyzed member. The reaction formula is normal, sensory disturbances are absent. In exceptional cases a high degree of atrophy may be present due in all probability, not to the functio lesio, but to the lesions in the trophic centers of the cortex, the exact seat of which is as yet undetermined.

BUFFALO, N. Y.
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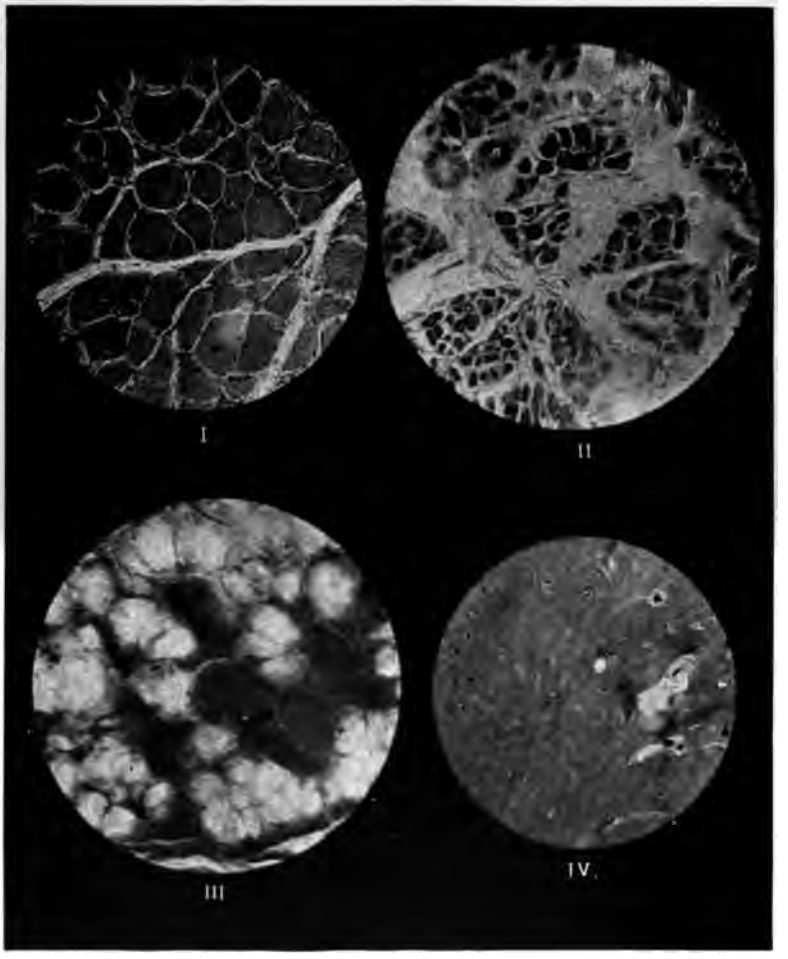

ILLUSTRATION OF MUSCULAR ATROPHIES—KRAUSS.

EXPLANATION OF PLATE.*

FIG. I. Cross-section of a normal muscle. Zeiss' E objective, No. 1 eyepiece.

FIG. II. Simple degenerative atrophy of a muscular fiber. Zeiss E, No. 1 eyepiece.

FIG. III. Fatty infiltration and degeneration of a muscular fiber. Zeiss E, No. 1 eyepiece.

FIG. IV. Destruction of the antero-lateral group of ganglion cells, ventral-cornua gray matter, spinal cord. The ganglion cells to the left (antero-median) are intact, while the antero-lateral have been replaced by cicatricial tissue. Zeiss E, No. 1.

* See author's paper on Muscular Atrophies, Buffalo Medical and Surgical Journal, April, 1891.

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THE BRAIN OF DIEMYCTYLUS VIRIDESCENS, FROM LARVAL TO ADULT LIFE AND COMPARISONS WITH THE BRAIN OF AMIA AND PETROMYZON.

SUSANNA PHELPS GAGE.

The remarkable changes in habits, appearance, structure and physiology which occur at two distinct crises in the life history of *Diemyctylus viridescens, Raf.*,* suggest the question whether any corresponding changes in the brain occur at these periods. Part I is a partial answer to this question.

In order better to understand and homologize certain parts and regions of the diemyctylus-brain comparisons were made with the brain of amia and of larval lampreys. The second part of this article deals with these comparisons and the general conclusions drawn from them.

PART I.

THE BRAIN OF DIEMYCTYLUS.

In order to answer the question stated above the brain ot diemyctylus has been studied in its various stages of development (16).† A few ova were prepared—effort was mainly directed, however, to the stages following hatching;—the very young larvæ (Fig. 12); older gilled larvæ which are half grown and ready to transform; the gill-less red form in three stages of growth, and finally the adult viridescent form (Fig. 11), male and female of various sizes.

The investigation has been confined almost exclusively to parts which in larger brains can be studied more or less perfectly by macroscopic sections and dissections. The purely

* Spotted triton or newt, vermilion spotted salamander (16).

† The numbers in parenthesis refer to the bibliography.

histological studies necessary for a complete investigation have not been made.

METHODS.

As the brain is small—6–7 mm. long in the adult—only a few general facts can be arrived at by its study as a whole. The skull is extremely hard, and the removal of a fresh brain is difficult, hence specimens in which bone was developed were decalcified and sectioned through the entire head (17).

The specimens were killed by chloroform or strong alcohol, put immediately into picric alcohol, hardened in 67 and 82 per cent. alcohol, dehydrated and cut in collodion. Hæmatoxylin and a variety of carmine stains were used. The nerves and larger nerve tracts are well marked, and in some series the deep origin of nerves can be traced with great distinctness, while the natural relation of parts to each other and to the membranes is left undisturbed.

Only young larvæ needed no decalcification. A few brains were removed and prepared by a modification of Golgi's method. Embryos were hardened in Perenyi's fluid after removal from the egg capsule.

About 70 series of sections of the head were made. Groups of three specimens agreeing as nearly as possible in size and development, were cut in the three planes, transverse, sagittal and frontal, in order to correct errors due to loss of substance in cutting and to ensure the natural arrangement of parts in drawing.

The photographic reproductions in Plate 1 show the character of the material, the eye only, of the macroscopic parts, is imperfect, the lens being so hard that its removal was necessary. Cilia, when present, were perfectly preserved in the mouth and nasal cavities, but were not found within the brain cavities. Whether this is due to their absence or the retarded penetration of the hardening agents is not known; other details of structure are clear.

HISTORY.

The brain of diemyctylus has been little studied. Mason (32) shows by a photographic process a transection through

the geminums and a fragment of the cerebrum to illustrate histological structure. Burckhardt (6) in comparing the brain of Ichthyophis with Triton, bases his main conclusions upon the European forms of triton, but records a few observations upon the American form, diemyctylus. His adult material was hardened and decalcified in a mixture of chromic and nitric acids and cut through the entire head. His general conclusion with regard to the urodeles may be summarized as follows (p. 400): They are uniform in the non-existence of a neck-flexure, and in having a small pons-flexure. The mesencephal appears like the myel in section. The diencephal loses its connection with the epiphysis which becomes functionless. The olfactory lobes are not distinct from the cerebrum and the latter has no temporal lobe. The double root of the olfactory nerve he considers of small phylogenetic moment. He considers that in this group a reciprocity exists between the size of the united rhinen- and prosencephal and the united dien- and mesencephal. In the only specific references to diemyctylus (p. 372), he says that the two former equal in volume the two latter, that the mesencephal swells out into two corpora bigemina, and that, as in all tritons, the mesencephal has a sulcus dorsalis (p. 377). With regard to the general statements given above the observations in this article in the main agree. Neither of these authors have touched upon the problem stated above, and a number of matters are described and illustrated in this article which have hitherto not been recorded.

A preliminary paper containing some of the points here given was presented at the American Association for the Advancement of Science (18).

BRAIN OF THE ADULT. PL. II–V.

In general outline and proportion of parts the brain of diemyctylus differs little from the other urodeles as shown by Osborn and others. The united hemicerebrums and olfactory lobes form the most conspicuous part of the brain and overlap the diencephal which with the mesencephal forms a rounded body. This in turn overlaps the metencephal,

the cerebellum being nowhere visible from the surface. The metaplexus forms a conspicuous object on the dorsal side. The supraplexus is not very large and lies between the caudal angles of the hemicerebrums; immediately behind it are the habenæ and the small epiphysis. On the ventral side, the diencephal with its connected infundibulum and hypophysis, covers the floor of the mesencephal.

In the mesal view, the cerebellum appears; the thickness of the parietes, the relations of commissures, cavities and plexuses are also seen.

In the figures, interrupted lines indicate the extent of the cavities which are wide, especially in the dorso-ventral direction, as seen in sections (Pl. III). The constrictions of the cavities are so great, that sections, which like those of Pl. I show them as continuous from cephalic to caudal extremity, are rare.

Rhinencephal.—As in other urodeles the olfactory lobes are entirely separate from each other. From the ectal surface there is little appearance of constriction separating the olfactory lobes from the hemicerebrums. The cavities show a slight dorso-lateral constriction (Fig. 5,) in frontal view seen in figure 37. A decided angle exists at the caudal boundary of the rhinocœle (Fig. 35, 41), which corresponds almost precisely with the caudal boundary of the second olfactory nerve root. Hence it is seen that the rhinencephal is nearly equal in length to the prosencephal.

The paraplexus intrudes slightly into the rhinocœle. The extensive area occupied by the external origin of the olfactory nerve roots is noticeable and the fact that a fold of pia intrudes between the two roots.

Cinerea covers nearly the entire surface of the olfactory lobes. But it is a remarkable fact that at certain points the ectal cinerea is continuous with the ental (Fig. 14–15, 35–37, 41) as though the embryonic condition were preserved.

Prosencephal.—The hemicerebrums have a decided though short caudal projection (Fig. 19–22), beyond the portæ, containing a spur of cinerea (Fig. 36, 42) which corresponds in position with a similar spur which Edinger (11, p. 20) has found in rep-

tiles. This he calls Ammon's horn as it connects with olfactory nerve fibers and represents the cortical olfactory center of higher forms. Whether a similar connection and function can be demonstrated in diemyctylus is not known.

The paraccœles open by wide portæ into the aula (Fig. 17, 36, 37). The cavity of the latter is nearly filled by a plexus, auliplexus (p. 265), so that the portæ are not visible from the meson (Fig. 6).

The caudal limit of the aula is defined by a band of alba or white matter rising from the floor of the brain, in the terma. This is formed by the cerebral commissures. The more dorsal portion is the *callosum* (38, 42), which in the form of a horseshoe sends lateral columns dorsad (Fig. 6, 18, 19, 42, 51) into the mesal walls of the hemicerebrums (Fig. 35–37).

These mesal walls of the hemicerebrums as they bulge into the cavity of the paraccœles have sometimes been called striatums, in amphibia. Osborn (38, Fig. 9) shows the fibers of the callosum distributed in this region of the frog to "the upper median cell area," while in reptiles and birds he found in this region a "sulcus" or fissure, the hippocampal. Nakagawa (35) considers the cells of this region in spelerpes to be a rudimentary cortex. In diemyctylus this region is clearly defined, contains numerous, but well separated cells in large pericellular spaces (Fig. 41, *c e.*), extends from the rhinoccœle to the portæ (Fig. 36) and caudad over the portæ to near the tip of the cerebrum (Fig. 21, 35). The fibers of the callosum spread out between these cells. There is no indication of a fissure but it seems proper to use the term *callosal eminence* to indicate this ridge pushing into the paraccœle, as it corresponds in position to that eminence as shown by Wilder (55, Fig. 4748) in a human fœtus.

In figures 17–19, 51, angles in the paraccœles are seen associated with projections of cinerea which form two horns curving outward and toward each other. This enclosed, lateral region of the cerebrum, through which the fibers of the precommissure pass, may be considered as a very undeveloped form of *striatum* —inasmuch as in other forms this region has been so homologized.

The *precommissure*, as seen upon the meson (Fig. 6), is closely associated with the callosum, but a little distance on either side three bands of alba appear (Fig. 51), the dorsal, the callosum, the other two, parts of the precommissure (38).

Diencephal.—Caudad of these cerebral commissures and partly underlying them is the *preoptic recess* (Fig. 18), a slight pocket in the endyma of the terma, which is continuous caudad with the small recesses extending slightly into the roots of the optic nerves. The cinerea about these processes is continuous in the center of the nerve to its entrance into the eye (Fig. 40), though no lumen is visible.

The chiasma (Fig. 6) projects into the diacœle and does not project below the general level of the ventral surface. Whether the part marked chiasma also includes an inferior commissure is not certain, but seems probable, as it has been found in *Triton alpestris* and other urodeles.

The *infundibular* region is large as in other low forms, and has wide lateral processes of the cavity which underlie the saccus. The *saccus* is formed by an irregular tubular arrangement of cells, corresponding in appearance to the endymal cells of the vicinity. The continuity with endymal cells is probable, and is so represented in figure 23, but is not an absolutely established fact. Among the tubules are capillaries. The saccus is small in comparison with other amphibia and fishes (cf. Fig. 93). In other series than those represented, no such tubular arrangement was found, the roof of the infundibulum being composed of a single, simple layer as though not thrown into folds to form a saccus.

The *hypophysis* is distinctly tubular and appears to be enclosed by pia which separates it from the infundibulum, as Osborn (37, p. 264)found in Cryptobranchus. Pigment cells from the dura are also seen to intrude between them in frontal sections (Fig. 50). In one heavily pigmented specimen such cells completely separate the hypophysis from the infundibulum. The floor of the infundibulum dorsad of the hypophysis is wide and composed of a single layer of endymal cells. No indications of hypoaria as in fishes (Fig. 93) were found.

The *thalamus* (Fig. 19–22, 37–38) is not sharply defined

from the striatum; its endymal surface is marked by sulci, one of which extends from the porta to the infundibulum—another continues caudad as the widest part of the mesocœle, another lies ventrad of the enlargement of the habena (Fig. 20–22).

The roof of the diencephal (Fig. 52) is separated caudad from the mesencephal by the postcommissure. Cephalad of this are, (1) the simple layer of endyma which underlies (2) the epiphysis, (3) the supracommissure connecting the habenæ (Fig. 59–60), and (4) a layer of flattened cells passing cephalo-ventrad from the supracommissure and reflected over the diaplexus. This order agrees with that now usually accepted and not with that mentioned by Edinger (10, p. 37) in which he places the connection of the epiphysis with the roof cephalad of the supracommissure.

The epiphysis is insignificant (see p. 285). The supracommissure (Fig. 52) is traversed by processes of the endymal cells covering it.

Plexuses.—The *supraplexus* is seen on the dorsal surface of the brain (Fig. 4). It is a complicated coil of blood vessels connected with the blood supply of most of the cephalic part of the brain. Vessels lying in the intercerebral pia (Fig. 6, 7), and vessels extending between the cerebrum and thalami unite with it (Fig. 21), and from it are supplied the two plexuses entering the brain at this point. Within its coils lies the paraphysis (Fig. 6, 52, 59), (see p. 286). The opening of the paraphysis indicates the division between two plexuses which are here named from the place at which they enter the cavities the *auliplexus* and the *diaplexus*, in preference to the terms of Burckhardt (6). He calls the same things in Ichthyophis, superior, inferior and medius, making three divisions instead of two.

Figure 6 shows these two plexuses from the meson. The diaplexus extends sometimes to the cerebellum or even farther, or sometimes is found with its tip pressed close to the postcommissure. Its blood supply is from the caudal side of the opening of the paraphysis, while the auliplexus receives its supply from the cephalic side (Fig. 7). The latter at its en-

trance to the aula dips ventrad, separating the portæ (Fig. 17), and gives off from its dorsal part the two paraplexuses (Fig. 42) which extend even into the rhinocœles. Dorsad of the callosum it is constricted but continues caudad into the diacœle (Fig 22) where it becomes much expanded and falls into the infundibulum.

Mesencephal.—There is no marked stricture between the mesocœle and the diacœle though the postcommissure and the origin of the 3d nerve may be considered as approximately determining the division.

Ventrad of the postcommissure are seen cells differing in character from any others of the endyma, having a wide clear margin, and together forming in section, a lunular mass on either side (Fig. 59, 60, 9, 10). From these cells fibers appear to take origin which become incorporated in the postcommissure. Sections prepared by the silver method were defective in this region and hence proof of the connection of the fibers with the cells is not positive.

In lamprey (Fig. 110), similar cells are found but the masses are farther separated by the postcommissure. To the cells similar in appearance, but underlying the habenæ, Edinger (10, p. 20) ascribes a secretory function, while Rabl-Rückhard (41) homologizes such cells in some amphibia, reptiles and birds with the torus longitudinalis of bony fishes (see Fig. 100). In section, the mesencephal is oval with such a slight depression on the dorsimeson (Fig. 25) as hardly to justify calling it a sulcus, as does Burckhardt (see p. 261), and except for uniformity the term geminums does not seem applicable. The cavity is oval except at its caudal part (Fig. 26) where it becomes a mere slit. There is no special lateral expansion at either cephalic or caudal part, and hence no indication, in the adult of lateral recesses. The dorsal union of the geminums is wide, the cinerea occupying the ventral half, with more scattered cells in the alba of the more dorsal portion. These cells extend to the extreme dorsal limit, but only upon a mesal plane (Fig. 25, 26), (see p. 293). From these cells the cinerea extends on either side in three somewhat illy defined concentric layers (Fig. 24–26) as Nakagawa (35) de-

scribes in Spelerpes, not in the clearly separated layers of cinerea found in the frog (Osborn).

Epencephal.—Projecting far cephalad under the mesencephal is seen the *cerebellum*, with bands of white matter crossing the meson (Fig. 6, 26, 36, 37). The origin of the 4th nerve at this point is the only indication of a *valvula*. Laterally the cerebellum is larger than on the meson (Fig. 26) and projects into lateral recesses which are continuous with the metacœle. The origin of the 5th nerve from the floor of the recess indicates that its more cephalic portion at least may be counted as belonging to the epencephalic segment and perhaps it represents the lateral recess (parepicœle) of the epencephal of higher forms.

Metencephal.—All of the nerve roots belonging to this segment from the 6th to the 12th, were found and their ectal origin is indicated on figure 5. For a further consideration see p. 273.

The *metaplexus* forming the roof of the segment is large, and for convenience will be considered in two parts, as the appearance changes. The cephalic part is wide and has a mesal fold dipping into the metacœle. On either side of the fold is a series of pockets lined by endyma and connected with the metacœle (Fig. 27, 35). The pockets radiate from the mesal fold of this portion of the plexus. A blood vessel lies in the median fold, and connects with others between the pockets. The spongy portion of the plexus thus formed is bounded caudally by a spicule of bone which crosses the meson (Fig. 6, 28). Ventrad of the bone and in the region of the origin of the 10th nerve, the dorsal walls of the metencephal become approximated and the plexus narrow and simple (Fig. 28). This is a strong reminder of the fish-like condition where in a corresponding region the walls touch or actually unite across the meson (Fig. 93 of amia). The caudal portion of the metaplexus extending from this point again widens (Fig. 29), and retains its simple character. Just cephalad of the closure of the myel, the endyma and pia of the metaplexus are absent across the meson, thus forming a true metapore (see p. 279).

Membranes.—The *pia* forms a complete investment for the brain, but does not in all places follow the outline closely, frequently lying nearer the dura than the brain (Fig. 16). Between the hemicerebrums the two folds unite to form a single membrane within which the blood vessels run (Fig. 19). The pia invests the hypophysis separating it from infundibulum (Fig. 6), and is continuous over the epiphysis (Fig. 22). The blood vessels in the pia are numerous, as are also the capillaries penetrating the brain. The latter usually enter the brain and return by the same path (Fig. 51), thus forming a close loop, which extends deep into the alba, as at the callosum (Fig. 51). The capillaries extend to but not into the entocinerea, passing between cells of an incipient ectocinerea as in the olfactory lobes and the callosal eminence (Fig. 17). Plate III shows the number and extent of the loops accurately.

Whenever the pia is separated from the brain, it is seen that upon the surface of the latter nuclei indicating cells occur at some little distance from one another, and that the surface is clothed with filaments extending toward the pia (Fig. 51). Stieda (47) found such filaments in the frog. Examination of sections stained by Golgi's method, from the mesencephal, where this condition is clearly defined, shows that cells lie at frequent intervals among the bases of these filaments (Fig. 61). The cells give off processes extending at least to the cinerea, while other cells scattered in the alba give off processes toward the endymal cells. In some sections the processes from two cells in these different situations unite or at least touch. In the larvæ (Fig. 62) similar filaments are seen bridging the space between the brain surface and the pia.

The *arachnoid* is represented by connective tissue cells lining the dura, and forming a spongework in the larger spaces existing between the dura and pia, notably in the triangular dorsal and ventral spaces existing between the pia of the two hemicerebrums (Fig. 6, 14); in the large spaces laterad of the mesencephal (Fig. 22), and in the region of the metapore (Fig. 29).

The *dura* is a membrane, containing numerous large pigment cells (Fig. 52, 55), lining the cranial cavity; sending

off an almost complete investment for the supraplexus (Fig. 51, 53), a somewhat partial one for the hypophysis (Fig. 50, 23); filling a large space (Fig. 28) caudad of the more spongy part of the metaplexus; surrounding the protrusion of the endolymphatic sacs into the cranial cavity (Fig. 8); following out the nerves from the cranial cavity (Fig. 40, II) and surrounding their ganglia (Fig. 24, 39).

The *endolymphatic sacs* (Fig. 8) unite by a tube with the ear, appearing as Norris (36) has shown in amblystoma. They extend cephalad each side of the mesencephal (Fig. 35–37, 23–27), with diverticulums passing caudad of the mesencephal approaching each other over the metaplexus where the cavities of these sacs and of the brain are brought into very close contact (Fig. 37). In one specimen the sacs unite over the meson (Fig. 34) as they are said to in the frog. By injection methods Rex (43) has studied the grosser vascular supply of the brain of *Triton cristatus*, and as far as the diemyctylus has been studied it agrees closely with his results.

Intermaxillary gland.—Cephalad of the brain, between the nostrils, with its tubules very close to the nasal epithelium is the intermaxillary gland with its duct opening into the mouth between the choanæ (Fig. 6, 35–40). Wiedersheim (49) attributes the discovery of this gland to Leydig, and gives a full account of it. In the urodeles it extends farther caudad than in the anura, but he shows no such close apposition to the brain as occurs in diemyctylus. Here the tubules ramify very close to the brain not being separated from it by a bony wall for some distance on either side of the meson. The combined meninges in this situation are delicate. In fact its sepation from the brain is only slightly more pronounced than that of the hypophysis. Its nervous supply is apparently from a branch of the 5th which crosses the olfactory nerve (Fig. 41). In young larvæ the gland does not appear, but before the end of the gilled larval stage it is well developed. In the red forms it reaches its maximum development in correlation with the greatly exaggerated glandular growths in the skin. In this stage its greatest usefulness would be expected as the secretion in other species is said to aid in securing food by mak-

ing the tongue viscid. In aquatic forms such a viscid secretion naturally would not seem of much use, at least the appearance of the gland in the adult seems to justify this conclusion for its tubules are more shrunken and its cells have less the appearance of activity. A further comparison of this gland in the different groups of amphibia seems desirable.

BRAIN OF YOUNG LARVÆ. PL. I. VI, VII.

The larvæ, the brains of which are figured, were about 1 c m. long—were only a few days from the egg, had lost the "balancers;" the eyes were large, the pectoral limbs formed; they were active and responded promptly to any jar of the water. Food was found in the stomach and a thoroughly independent existence was established.

The description of Plate I serves to compare the adult and larval brain as seen in frontal section. A comparison of figures 4 and 64 shows the marked differences in external form. The olfactory lobes and cerebrum together are relatively short, and the cerebrum is overhung by the diencephal with the habenæ. The united dien-and mesencephal form a more marked feature of the brain; the mesencephal still farther overlaps the metencephal; large as the infundibular region is, it is almost enclosed by the cephalic extension of the lateral wings of the epencephal which project far laterad also (Fig. 64–65). In general the argreement of the larval diemyctylus with amphiuma as described by Kingsley (30) is very close.

The cells composing the cinerea are much larger than in the adult, and in many places are distinctly arranged in rows radiating from the endyma (Pl. VII). This arrangement exists in the adult (Fig. 51) but does not show with low magnification. The alba of the larva is small in quantity relatively—being massed at the sides—with a small amount crossing the meson (Fig. 6, 67).

Rhinencephal.—The olfactory lobes are less separated from the hemicerebrums than in the adult, though the caudal limit of the former may be determined by the position of the second olfactory nerve root which is present. Cinerea occupies a large portion of the lobes and the continuity of ectal with ental cinerea is extensive.

Prosencephal.—The cerebrum is markedly undeveloped, especially in the region of the callosal eminence (compare Fig. 35, 69; 36, 2; 37, 71; 16, 76). Owing to this the terma and hence the portæ have their cephalic boundary at a level with the caudal portion of the olfactory lobes. The lack of development of the callosal eminence is correlated with the fact that barely a trace of the callosum is seen (Fig. 91), a few fibers appearing on each side and even fewer crossing the meson. The combined callosum and precommissure do not rise much from the general level of the floor of the cavity (Fig. 67). The precommissure is foreshadowed by the two small white areas crossing the meson, while the striatum (Fig. 16, 78) shows one lamina of cinerea instead of two as in the adult.

Diencephal.—The chiasma and optic nerves are well developed as would be expected from the condition of the eyes.

The infundibulum is much compressed cephalo-caudad and no alba is developed in it (Fig. 81, 22). A saccus is not formed, and the hypophysis is minute (Fig. 82). The roof of the diencephal presents the same relations as in the adult, but the opening between the supra- and postcommissures into the epiphysis can be traced (Fig. 68). The epiphysis is relatively larger than in the adult but its cavity is much depressed.

The habenæ are relatively very large (Fig. 4, 64), they extend far cephalad and partly overhang the paraphysis (Fig. 78, 91), and except for intervening pia they present a large area upon the meson (Fig. 67).

Plexuses.—The *paraphysis* is an almost straight tube with an enlarged end (Fig. 67, 78, 79), surrounded by a few cells and small vessels which constitute the rudimentary supraplexus, and have the same relation to the other plexuses as in the adult (Fig. 66, 67). The dia- and auliplexuses have the same relative position and extent as in the adult, but the endyma with which they are covered is undifferentiated from other endyma and the contained blood vessels are minute. The paraplexuses arising from the auliplexus are small (Fig. 78), and do not extend into the caudal part of the paracœles as in the adult (Fig. 21).

Mesencephal.—This differs considerably from the adult. From the dorsal aspect (Fig. 64) a broad band of cinerea is visible, while in the adult only a very limited area at the caudal end is seen (Fig. 4). This is part of the ental cinerea which has not yet been covered by the growth of alba. The cavity also differs in form, since at the caudal end a very wide lateral expansion exists (Fig. 84) which later entirely disappears (Fig. 26). This early character resembles the post-optic expansion of the frog, reptiles and birds.

The middle and cephalic portion of the cavity (Fig. 81–83), shows a narrow extension to the roof. The extent of this narrow portion is shown by the more lightly shaded portion of the mesocœle in figure 67. The roof in this part consists of a single layer of endymal cells, but it is evident that the closely approximated sides are in process of union. This process is complete in the adult, a mere trace of the past history being retained in the scattered cells which hold their place in the alba (Fig. 26).

Epencephal.—The cerebellum upon the meson is very small (Fig. 67) and shows only a trace of alba (Fig. 84), yet laterad it is larger (Fig. 83). The lateral recesses of the epicœle extend far cephalad. The relations of the cavity and the 5th nerve shown in figure 82 seem to confirm the conclusion that this cavity with its lateral recesses must be assigned to this segment rather than to the metencephal, though the relations are more obscure in the adult. The lateral wing of cinerea seen (Fig. 25) in the adult apparently indicates the partial closure of the cephalic portion of the epicœle. Figures by Herrick (24) of the sturgeon's brain in this region show clearly the relations which in amphibia are very obscure, and are confirmatory of the above conclusion.

Metencephal.—From the dorsal side, this segment shows a broad band of cinerea (Fig. 64) upon either side of the plexus. This almost disappears in the adult (Fig. 4).

The metaplexus is wholly undifferentiated being formed of a simple layer of cells not much different from the other endymal cells, and over it a few mesodermal cells which probably belong to the pia (Fig. 86–88). There is no indication of a metapore.

Membranes.—The pia is a very delicate membrane, in many places clinging closely to the dura. Its relations are the same, as far as traced, as in the adult, it supplies comparatively very few blood vessels to the brain; a few in the olfactory region (Fig. 75); in the region between the mesen- and epencephal (Fig. 82); and to the medulla (Fig. 85). Contrast the capillaries of Plates III and IV with VII.

The arachnoid is represented by a few connective tissue cells, and can be clearly seen only in the cephalic region in the triangular spaces between pia and dura (Fig. 75).

The dura is thin, and in the dorsal part where the cartilage of the skull is not developed, lies in close contact with the epidermis. In this part a few pigment cells exist.

The endolymphatic sacs are slightly developed and appear in only a few sections (Fig. 83, 84), they are closely applied to the lateral recesses of the epicœle but do not extend over the metaplexus. The canal connects it with the ear more directly than in the adult.

Nerves.—The methods, as stated, are not especially adapted to the study of nerve tracts, hence little beyond the external origin is mentioned. The relations in the larvæ are often clearer than in the adult.

I. The olfactory nerve in both young and adult has two lateral roots; in the latter a whorl-like arrangement of cells is seen in the lobe and more proximal part of the roots, that is not present in the larva. The roots unite to form one trunk which divides, sending branches to surround the nasal epithelium and to Jacobson's organ. These observations agree with Burckhardt (6) rather than with Kingsley (30), who found only one root in larval amphiuma.

II. The optic nerve is similar in larva and adult; the central cells of the larva occupy a much larger proportion of the nerve. In both, at the exit from the brain there are no fibers on the dorsal side of the nerve (Fig. 20); the fibers twist dorsad and soon form a complete tubular investment for the cells. The chiasma is well developed.

III. As shown in figures 23, 44, 38, 81, this has the usual place of origin. In the larva the commissure across the meson is cut off from other alba by cinerea (Fig. 67).

IV. Though small in the adult, this nerve is clearly seen (Fig. 26). In the larva a few cells (Fig. 84), probably indicate its rudiment, for in the next older stages it can be found. In the adult, the 3d and 4th nerves escape from the skull by separate foramens (Fig. 3). In the larva only one foramen through the cartilage is seen, and through this the 3d leaves the brain. Kingsley (30) did not find this nerve in larval amphiuma.

V. This has its origin at the usual place ventrad of the lateral recess of the epencephal (Fig. 39, 40, 25). Figure 44 shows fibers arising near the origin of the 3d, which extend to and unite with the fibers of the 5th. In the larva this nerve and the lateral recesses are far cephalad (Fig. 6, 82).

VI. The origin of this nerve is caudad of the 8th and upon the ventral side (Fig. 63). It is very small even in the adult (Fig. 25), but can be traced latero-cephalad to its union with the gasserian ganglion. In the larva only a mere trace of it was distinguished (Fig. 85) at its origin. This nerve is in amphibia so small as to escape observation, or it is variable in position. Kingsley (30) says it is not found in larval amphiuma; Reissner (42) shows it in the frog; Ecker (9, p. 149) figures it at the level of the 10th in the frog; Fischer (13) in siredon near the 7th; Osborn omits it entirely from some of his figures.

VII, VIII. In the adult these two nerves are very closely connected, as are their ganglia. The 8th, however can be said to be cephalo-ventrad of the 7th at its origin (Fig. 3–5), and comprises fibers only (Fig. 26), some of which cross the meson. The 7th at its origin has a great dorso-ventral extent, the more dorsal part extends from the sulcus (p. 291) (Rautenlippe of His), existing between the solid and membranous portion of the metencephal, and is cellular in character. The more ventral part consists of fibers (Fig. 8). There is no space between the fibers of the 7th and 8th, which pass into the united ganglion. In the larva the origin of the 7th and 8th are quite separate; the cellular portion of the 7th is continuous with the cinerea about the sulcus on the one hand and the ganglion on the other; while the

ganglia of the 7th and 8th are distinct (Fig. 83, 84, 92), the latter being more ventrad. In the adult, from the 7th a branch extends to the gasserian ganglion (Fig. 3, 4), and from the united ganglion a branch, said to be a part of the 7th, extends through the cephalic part of the ear, and branches are distributed to the sensory epithelium of the ear (Fig. 40). The observations recorded seem to agree with Ayers' studies (2). Strong (48) says that in amblystoma a branch of the 7th which innervates the lateral line, disappears when the animal adopts a terrestrial life. In diemyctylus, with the return to aquatic life, in the adult male, pockets are formed at the side of the head (Fig. 40, II) which receive branches of the 7th. There has not been time to study the changes of the nerve involved, but it is possible that here is a fruitful line of work upon the post-embryonic changes in a nerve.

Gasserian ganglion. In the adult two branches of the 5th and a branch of the 7th can be traced into and through this ganglion which lies within the skull and close to the endolymphatic sac (Fig. 3, 23, 39). In the larva the ganglion is deeply lobed (Fig. 63), the two cephalic portions are connected with branches of the 5th, the more caudal with the branch of the 7th.

IX, X, XI, XII. (Fig. 5, 65). The ectal origins of these nerves form a series each arising at a more ventral level than the preceding. The 9th is associated with a sulcus at the dorsal edge of the medulla, and the 10th with a more ventrally placed extension of cells, which according to His (26) would represent another sulcus which has been obscured by growth. This is clearly seen in the larva (Fig. 86). In the adult the 11th is seen to be an offshoot from a deep-lying bundle of fibers arising in the myel, part of which pass to the 11th and part extend further cephalad as the solitary bundle (Fig. 43). The origin of the 12th is far ventrad (Fig. 88). In the larva is an indication of a dorsal root (x in Fig. 65), such as is mentioned by Kingsley in amphiuma (30) and Froriep (14) in an embryo ruminant.

THE BRAIN IN EMBRYOS.

The incubation of ova in the laboratory lasted about one month. Within seven days, the optic and otic vesicles are formed. At twelve days the eyes, lens and rudiment of a nasal pit are formed and the brain in reconstructed mesal view agrees well with a figure of a newt shown by Misses Johnson and Sheldon (29). The partition between the prosen- and diencephal is formed and from this extends the dorsal division between the hemicerebrums. At fifteen days a protuberance of the diencephal (epiphysis) is formed and the infundibular region is partially constricted. No alba has appeared, the walls being purely cellular. A mesal view is similar to one by His (27) of *Ambhystoma punctatum*. At or near the time of hatching the eyes are large; the muscular development is excellent and suited to the quick darting motions. The yolk sac is large and the mouth not yet perforated. Balancers exist and the nasal pit is formed. The cephalic curvature still remains so that a transection in the cephalic region still shows the structures found in frontal sections of older forms. The united cerebrum and olfactory lobes are short, extend ventrad from the diencephal, which with the mesencephal forms the most cephalic and the most prominent portion of the brain. In the wall between the hemicerebrums, is the rudiment of the paraphysis (Fig. 73) and into the diacœle projects a rudiment of the diaplexus. In figure 74 the aula is seen to reach nearly to the tip of the rhinencephal. The mesocœle is a wide cavity, the lateral recesses of the epicœle are formed, and the lateral masses of alba are considerable, while, except in the medulla, little alba is seen on the meson. Within two days after hatching the cranial flexure has nearly disappeared.

BRAIN OF OLDER LARVÆ AND OF RED FORMS.

Before the end of aquatic larval life the general longitudinal proportions of the adult brain are attained, but the parts are more depressed dorso-ventrally while the cavities are large. This appearance increases until the middle red stage and corresponds with the general appearance of loose struc-

ture and growing spaces of this period. With continued growth the structures become more compact.

The growth of the mesal walls of the cerebrum is slow, the cells and alba forming the callosal eminence being gradually added until, before the adult stage is reached, it is fully formed. The callosum and precommissure continue to be separated by cinerea up to adult life, and even in some small adults the condition persists.

The compressed form of the *infundibulum* is lost by the middle red stage. The saccus is sometimes quite convoluted by the end of terrestrial life but this is apparently a variable condition. The hypophysis in the late red forms shows the tubules widely open, but the large relative size of the organ is not attained until adult life, though in the latter the tubules again are more compressed. The original close approximation of the *notochord* to the hypophysis (Fig. 67) is lost by the middle red stage. The *paraphysis* is nearly as convoluted in the small red forms as in the adult owing to the extensive development of blood vessels in the supraplexus which takes place at this stage.

By the end of aquatic larval life the roof of the *mecencephal* has coalesced, the broad dorsal band of cinerea remains through this stage, and fully grown red forms show a line of cinerea on the dorsal side where the union took place. (See p. 293). In the middle red stage the layers of cinerea are forming while in late red forms the layers are more clearly separated than in the adult—especially is the endyma separate from the next cellular layer. Traces of the caudal expansion of the mesocœle remain until late red stages (Fig. 8).

The cerebellum is as large proportionally by the middle red stage as in the adult, and at that time the extreme latero-cephalic projection of the lateral recesses of the epicœle has disappeared.

The metaplexus shows a median fold in a 16 mm. larva while a mere trace of the metapore has appeared and consists in the abrogation of a few cells of endyma (Fig. 57). In the large aquatic larvæ the metapore has not increased in size but the metaplexus is as complex as in the adult. By the middle

red stage the metapore is larger and by the end of terrestrial life the condition is practically the same as in the adult.

The pia and arachnoid are more clearly defined in the red stages than in others, as owing to the more rapid growth of the skull, the brain does not fill the cavity, and appears hung in sheets of pia and supported by a spongework of arachnoid.

In early stages the dura has only a few pigment cells where it is in contact with the epidermis on the dorsal side, these increase gradually ventrad but even in the large red forms where the pigment is scattered throughout the dura, it is small in amount and of a brown color. The great increase of pigment in the dura seems to be associated with large size in the adult, and in one very marked case, with a shrunken condition of the brain.

The endolymphatic sacs in the larval forms are small, in the red forms the relations of the parts are clearer than in the adult (Fig. 8) because the sacs apparently are not so convoluted.

Between the brains of the adult male and female there appears to be no difference other than occurs between individuals of the same sex.

SUMMARY.

From the above detailed description it is seen that the brain of Diemyctylus resembles, in its embryonic, young larval and adult stages, the brain in corresponding stages of other Urodeles; and that there are no marked changes in the morphology of the brain corresponding to the crises of development and change in structure and function of the animal. After the earliest stages of larval life, the parts of the brain develop gradually, one after the other acquiring its mature form, at periods which have no exact relation to those crises. There is, however, a marked general growth at about the time of final transformation so that the brain much more nearly fills the skull than in the late red forms.

The grosser morphological plan was laid out before hatching, the details are added by gradual growth. It is possible that in the finer structure of nerve cells, in the path of nerve

tracts, and their exact processes of growth, determined by finer methods, a more complete correlation of brain structure with these crises may be found.

PART II. PLATE VIII.

COMPARISONS WITH AMIA AND LAMPREY.

MATERIAL.

The brain in the skull of *Amia calva* was prepared, sectioned and drawn by methods described for diemyctylus. Twelve series of larval Petromyzon* were cut, some after hardening in picric alcohol, but the more successful preparations were hardened in mercuric chlorid.

The sections made agree in most particulars with the figures of Ahlborn (1) of lamprey and Goronowitsch (21) of the amia. The drawings presented add certain details, show somewhat different structure or are necessary to illustrate the comparisons here made. The reconstructed mesal views show certain features not before noted.

A detailed account of the figures is given in the explanation of Plate VIII, hence a consideration of special points will be at once entered upon.

METAPORE.

Wilder (54) has demonstrated that in the adult man and certain apes, in the caudal region of the metaplexus, there is a lack of continuity in the endyma and pia, thus placing the cavities of the brain in communication with subarachnoid spaces. In lower forms such an opening has been considered, from an embryological standpoint, as highly improbable, no such break being found in early stages. In the amia (Fig. 93) a pocket of endyma extends caudad from the metaplexus

* It is impossible to state whether these were larvæ of Petromyzon marinus or of Ammocætes (Petromyzon) branchialis, since both lay their eggs in the same streams and even the same nests, as shown in an article by S. H. Gage in this volume.

over the cephalic end of the myel. In transection it has a considerable lateral extent. The lamprey may be considered to have a very small sac in a corresponding position (Fig. 111) as, just cephalad of the closure of the myel, the walls approximate closely, the endyma being in contact except at the dorsal limit where it swells out into a minute sac. In neither lamprey nor amia was any lack of continuity in the endyma seen. Rex (43) in this region of the elasmobranchs shows that the vessels leave a little space at this point, though all around they form a close meshwork, and Burckhardt (8) shows a sac similar to amia in protopterus.

In diemyctylus such a pocket was not found nor, in the earliest stages, any lack of continuity of the endyma. In a half grown aquatic larva the last section before the closure of the myel shows that the endyma of the plexus is not complete and the pia does not cross the meson, though in the section on either side these conditions do not exist. This same condition was found in various series up to a full sized red form. In a large red form and all the adults examined which were perfect in this region the opening was much more pronounced, and was observed in sections cut in different planes (Fig. 54–56). Here the pia with its vessels extends toward the opening but not across it, and the endyma is recurved at the lateral and caudal margins, but suddenly ceases, leaving a free communication of the cavity with a subarachnoid space. It may be objected that the cells lining the pigmented dura are endymal cells, but they do not have the size nor appearance of endymal cells and furthermore form a continuous layer lining the dura in its whole circumference and are united by connective-tissue like cells with the pia at frequent intervals as in figure 55, *ar*. The recurved endyma may represent the remnant of a stage like the amia.

After the most careful study of the sections, which show no indication of tearing, delicate connective tissue cells and processes retaining their position, the conclusion is unavoidable that a true metapore exists in the adult diemyctylus, and that its beginning or initial form arises in the larva.

INFUNDIBULUM.

Since the investigations of Müller in 1871, not much of fundamental importance has been added to the knowledge of this region. It is thought desirable here to compare the extreme variation in position of homolgous parts and to contrast the simple and complex character of the region in different forms. It seems that to give these parts collectively the name of a lobe as has been done is misleading, but that the term, infundibulum, long employed, may be used, apart from its strict etymological significance, with reference to the whole region and its appendages.

In the amia a cephalic projection of the cavity is associated with the hypophysis (Fig. 93, 98) as is also the case with lamprey (Fig. 103). In diemyctylus the whole infundibulum extends caudad but the hypophysis is associated with the part next the chiasma (Fig. 6).

In amia from the caudal part are four projections of the cavity (Fig. 93, 100); the two dorsal are symmetrical, and extend into the hypoaria; next a mesal cavity, short in extent; ventrad a longer extension, the saccus, with walls of different structure, apparently non-nervous. In lamprey only one caudal process exists (Fig. 103, 108), while in diemyctylus the relations are obscure. There is a small lobular process which in position corresponds with the saccus but the membranous wall dorsad of it more nearly in structure resembles the saccus (Fig. 6, 50).

CEREBRAL COMMISSURES.

The variations in position of these commisures both with relation to the brain masses and to each other seem to present one of the most puzzling problems to be solved in comparative neurology. The work of Reissner (42) and especially of Osborn (38) in determining the existence and relations of the callosum in im-mammalia clearly showed these variations, the position of the callosum and precommissure in urodeles being much more like that in fishes than in anura. In the latter the conditions are not dissimilar to those shown by Marchand (31) as

existing in the early human embryo, and also found in the lower mammals. Transitional forms must be looked for between the urodele and anurous conditions probably in embryonic forms.

In the larval diemyctylus the position of these commissures (Fig. 6, 91) even more than in the adult (Fig. 6) differs from the frog in relation to the terma. In this and other urodeles and in fishes (Fig. 93) the commissures are at the caudal boundary of the large aula, the terma not rising directly from them as in higher forms to the dorsal part of the portæ, but again dipping ventrad and curving around the large portæ. This is a modification of the embryonic condition in which the aula extends, as the common cavity of the cerebrum, to the cephalic extremity of the brain. It is as though the progress of the caudal development of the mesal walls of the cerebrum, carrying the terma with them, were arrested in the urodeles. Evidence of such a history is found in the larva and the adult in the cinerea which reaches the mesal surface, cephalad of the terma. In the young larva this consists (Fig. 67, 76) of a single layer of endyma, which before the end of larval life becomes several layered and in the adult through a large part of its extent is a mass of scattered cells (Fig. 6, 15) reaching to the mesal surface.

In fishes the lateral and ventral curvature of the walls of the cerebrum (p. 295) introduces another element of difference. In amia no commissure was found cephalad of the compound one (*cm.* Fig. 93, 97) representing the callosum and precommisure. Herrick (22, 24), however, in certain teleosts and possibly in lepidosteus has found such a cephalic commissure which he believes to be the callosum. Ahlborn (1) shows a commissure which connects the olfactory lobes directly, the precommissure (Fig. 103, 104). In the present study of the lamprey brain, another band of alba in a position easily overlooked, as it lies ventrad of a deep projection, was found (Fig. 103, 105, *cm.*). This is more comparable in position with the commissures of amia and diemyctylus than is the precommissure, but it connects parts which seem homologous with the striatums rather than with the callosal emi-

nence. With regard to the position of these commissures; the lamprey brain is in closer relationship with the anurous than the urodele or fish type of brain, though, as was suggested by Wilder (52) from other considerations, the brain of lamprey is much like that of urodeles. It is hoped that the facts now known with regard to these commissures may be brought into harmony by further embryological study.

CRISTA.

In diemyctylus an object which, in comparison to the size of the brain, is large, projects on the meson, freely into the cavity of the aula, as shown both in transections and in frontal sections. In the section cephalad of the portæ (Fig. 16), it is seen that the endyma is reflected over a rounded surface, the crista, to form the last remnant of the partition between the hemicerebrums. In frontal sections its base (Fig. 45) joins the floor of the aula, but then projects into the aula and toward the cerebral commissures. It contains white fibers, apparently non-nervous, with a herring-bone arrangement on either side of a loop of pia which extends far into it (Fig. 46). Its dorsal side (Fig. 47) showing endymal cells in face view, retreats to the general level of the terma, except that a slight ridge extends dorsad from it (Fig. 37), and this ridge (Fig. 36) is the point from which the endyma is reflected to form the auliplexus and (Fig. 35) the mesal walls of the cerebrum.

In the larva (Fig. 71, 72) a trace of this structure is visible. Here, owing to the large aula, it is relatively farther cephalad. In the twelve-day embryos it is far cephalad, being the first indication of the restriction of the aula. In later embryos it still is far cephalad (Fig. 73, 74). In all these cases this projection bears the same relation to the rudimentary mesal walls of the cerebrum as in the adult, though, in the embryos, the auliplexus is not yet developed. Hence, morphologically it is the dorsal limit of the terma, a kind of fixed point beyond which the olfactory lobes and the cerebrum project in their growth and from which the auliplexus is reflected.

In the amia a structure which agrees in position with the

above is seen to rise between the hemicerebrums (Fig. 95, 96), and is the ridge over which the endyma is reflected to form the partition between the hemicerebrums, this partition being in reality a plexus in the aula—auliplexus. Caudad of the reflection of the auliplexus it projects as a ridge into the aula, gradually becoming lower, and contains fibers probably of connective tissue, which are directed toward a mesal blood vessel (Fig 96), extending into it as in diemyctylus. Rabl-Rückhard shows a ridge in this situation in a bony fish (40). No such structure was detected in the lamprey.

The discussion of this apparently insignificant part of the brain has been introduced under the name *crista*, since that term has been used by Wilder (53) to designate a small, rounded body, seen from the aula resting upon the fornix and dorsad of the precommissure, in the adult cat and sheep and human embryos. At his suggestion, sections of this region in the cat have been made. Figures 48, 49, are through the columns of the fornix. The only noticeable feature in the structure is the fact that it contains rows of cells which are arranged at right angles to those of the fornix and that pia is found between the columns of the fornix extending almost to the crista. If, as in the fornix and other situations, these rows of cells indicate arrangement of fibers, it is not improbable that fibers may be present here which represent those seen in diemyctylus. The pia is cut off from actual entrance into the crista by the close union of the fornicolumns, but the appearance is very suggestive of that in diemyctylus, though there is no complete likeness of structure. In position it seems comparable to that body in diemyctylus, as it lies in the primitive terma which is disguised by the growth of the callosum and fornix, between the portæ, near the point where the auliplexus is reflected, and in the same morphological relation to the precommissure; hence the term crista is used to designate the part in diemyctylus and amia, and if found in other forms will be a valuable landmark in determining the relations of aula and commissures.

EPIPHYSIS AND PARAPHYSIS.

In the roof of the brain two outgrowths from the cavities have been found in embryos of all groups, the epiphysis arising from the diencephal between the supra- and postcommissures, the paraphysis farther cephalad and variously said to belong to the prosen- and diencephal. From a morphological standpoint the importance of these organs has been considered great, hence many special articles have been devoted to them. The history and present state of knowledge concerning them has recently been discussed by Béraneck (5) and His (27). In brief, the epiphysis is said to develop variously in different groups, becoming the pineal or parietal eye of lizards and lamprey, the conarium of mammals, while in amphibia it is very degenerate and was first discovered by Götte (20). The fate of the paraphysis in the adult has been very uncertain. Observations of Hoffmann (28) are very suggestive with reference to the possible relation of the neuropore with the paraphysis.

Epiphysis.—As seen in the figures the epiphysis of diemyctylus like that of other urodeles is insignificant. In embryos it is prominent, in the early larval stages a remnant of its connection with the brain remains (Fig. 68) occuring as usual between the supra- and postcommissures. In the adult this connection has disappeared and its cavity is nearly obliterated. Figure 58 shows a few lacunæ in it and the fact that it is in a region of numerous blood vessels. From its caudal end a few fibers pass toward the roof of the mesencephal forming a picture (Fig. 52) which resembles the condition in the frog as shown by Osborn (37). From the degenerate condition it would probably be impossible to determine whether these are nervous or connective tissue elements.

In the amia as in other ganoids, the epiphysis lies to the left of the meson, owing to the greater development of the right habena (Fig. 97–99). In this specimen figured, which is nearly adult, the stalk can be traced to its union with the brain. This union is by a tortuous path owing to the crowding of the habenæ.

Since the researches of Ahlborn (1) showed the nature of the pineal eye or epiphysis in lamprey, it has been settled that its stalk retains its connection with the brain at least through larval life. This connection is very clear in the specimens studied (Fig. 103), but the nerve which Béraneck (5) claims to have found connecting the epiphysis to the mesencephal, was not seen. The pigment of the organ agrees with the condition said to belong to this stage of development by Beard (4), that is, it is white by reflected light. He says that in both earlier and later stages black pigment is found. The white pigment extends from the floor of the epiphysis into the hollow stalk for some little distance (Fig. 104, 105) then the stalk becomes inconspicuous and passes between the two habenæ, to its union with the brain at the left of the middle, but on a *morphological* meson (Fig. 103, 109).

Paraphysis.—In diemyctylus before hatching, a cross partition divides the prosen- from the diencephal and from this is another dividing the prosencephal into right and left hemicerebrums. This T shaped partition so formed is permanent. Into the space where the two bars join is developed from the brain cavity the first trace of the paraphysis (Fig. 73). This, from the curvature of the brain, is a cephalic structure. When the flexure is lost the paraphysis retains its relative position but becomes a dorsal structure (Fig. 67), the stem of the T is represented by the mesal walls of the hemicerebrums with intervening pia, the cross bar is the fold cephalad of the diencephal in which the supraplexus and paraphysis occur. In the larva the tube has an enlarged bulbous end (Fig. 66) and is composed of a single layer of cubical epithelium. Around this tube are a few small vessels and scattered cells, the beginnings of the supraplexus. Eycleshymer (12) identified and has given an excellent account of the paraphysis in amblystoma up to this point of development, but in 14 mm. larvæ he says its proximal cavity is obliterated. This is not the case in diemyctylus, for in the adult the connection with the brain cavity still exists though it is constricted. The cavity continues to increase in size but by the beginning red stage it is convoluted by the growth of blood vessels which press

upon it, and in the adult it is a very irregular sac lying in the midst of the supraplexus (Fig. 51, 53, 59, 60). The opening is upon the meson at a point between the blood vessels supplying the dia- and auliplexuses. (See p. 265). This opening cannot be said to be into either diacœle or aula but rather, anomolous as it may seem, to mark the boundary between the two, for the cells next it on the caudal side belong to the diencephal, on the cephalic side, to the aula. As Eycleshymer noted, the paraphysis is separated from the epiphysis for some distance, the precommissure, habenæ and a stretch of endyma and a plexus intervening between their openings (Fig. 6, 52).

The dorsal sac of fishes is a well known structure, it is large and conspicuous, and the pallium, the membranous roof of the prosencephal, is beneath, and united with it.

In the amia the pallium (Fig. 93) is a membrane overlying which are great numbers of blood vessels, with branches into the intercerebral plexus (auliplexus) and the intercerebral pia in a way perfectly comparable to the arrangement of vessels from the supraplexus of diemyctylus (p. 265). Partly thrust into this mass of blood vessles and convoluted by them—partly overlying them, is the dorsal sac, which as seen from the meson has a narrow connection with the cavity (Fig. 93, *par.*), but in transection has a wide orifice (Fig. 98). It is a pocket or sac of endyma reflected from the supracommissure with a diverticulum extending caudad over the supracommissure and habenæ (Fig. 99). The stalk of the epiphysis arising as it does caudad of the supracommissure is thus brought into contact with the dorsal sac and continues cephalad upon it or partly enclosed in it (Fig. 98) and from this arrangement the term *second vesicle of the Epiphysis* has been applied (*Zirbelpolster* of German writers).

As in amia and lamprey there is no partition dipping ventrad, between the prosen- and diencephal in which the paraphysis may be sought, the essential relations of the above parts must be considered. The pallium with regard to its vessels is comparable to the supraplexus, and its endyma to the membrane from which the paraphysis rises in the diemyctylus, (see

p. 293 and compare Fig. 93, 6). The caudal diverticulum of the sac many be compared to the thin layer in diemyctylus forming the cephalic boundary of the diencephal (Fig. 6, 68, 52) then the remainder of the sac meets the requirements of homology with the paraphysis of amphibia,—a thin walled diverticulum from the caudal part of the pallium, partly surrounded by bloodvessels and having the same relation to supracommissure and habenæ.

Balfour and Parker (3, p. 377) described in lepidosteus a large sac which they say is homologous with Stannius' sac in the sturgeon; a similar one was described by Wiedersheim in protopterus. Goronowitsch (21) has made the relations of this sac very clear in the ganoid, and Burckhardt (8) in the dipnoan brain. The conclusion with regard to the homology of this sac, above deduced in the amia, is confirmed by the figures and description of the former, while from Burckhardt's results it may be concluded that the dipnoan brain agrees even more closely in this respect with the amphibian. He shows a dorsal sac divided into a part which is cephalad of the supracommissure, and may be compared with the caudal diverticulum in amia (Fig. 99), and the layer of epithelium cephalad of the diencephal in diemyctylus (Fig. 68); and a so-called *conarium* separated from the above by a *velum*. His conarium, the Adergeflectknoten of other German authors—the supraplexus—is a large sac with blood vessels around it. The velum, though small, exactly corresponds in position with the diaplexus of diemyctylus, while from its cephalic border are given off the paraplexuses. Whether a true auliplexus exists cannot be determined from his figures, but in its essential relations his conarium seems to be the paraphysis of amphibia.

This second vesicle of the epiphysis as it is sometimes called, is a marked feature of the lamprey's brain, as of the reptile's. Ahlborn (1) shows it in lamprey lying ventrad of the epiphysis or pineal eye. He considers that the cavity of the epiphysis opens into the cavity of the second vesicle; that the left habena which extends as a white band far beyond the right to the second vesicle, forms the nervous

connection of the pineal eye with the brain. He says (p. 282) that some of his sections seem to indicate that an opening exists between the second vesicle and the brain cavity. Gaskell (19, p. 433) considers that the left habena serves as the nerve for this sac and the right as a nerve for the epiphysis.

From the present investigation no indication of the opening of the cavity of the epiphysis into the sac lying ventrad of it is found, in fact the two are separated by a connective tissue cushion and a blood vessel (Fig. 104, 105). Nor is there indication that the habenæ serve as nerves for either the epiphysis or this sac, though there may be a correlation of their unequal size with the comparatively developed condition of the epiphysis. The left habena (Fig. 105) extends under the epiphysis. At the right is seen a small cavity opening into the general cavity. This is the second vesicle and probably the opening which Allhborn considered as possible. Figure 104 shows a more cephalic section in which the tip of the left habena, covered by endyma, extends into the same cavity but maintains its lateral position with regard to it. The reconstruction of the cavity is shown in figure 103, where it is represented upon the meson though its opening is not exactly at the middle of the section. This is because an organ, the left habena, which is admitted to be morphologically a lateral organ, has, from unequal growth, assumed a mesal position and pushed aside a small mesal structure.

From the relation of this second vesicle to the habena, and the supracommissure, from its morphologically mesal position, and its relation to a blood vessel dorsad of it, I conclude that it is the paraphysis, even though no plexuses in the brain serve further to determine its identity. This is in consonance with the statement of Scott (46) that in the earlier stages of petromyzon, the two dorsal vesicles are soon pushed to the left of the meson ; and of Goronowitsch (21) that in *Acipenser ruthenus* the habenæ and dorsal sac are asymmetrical.

In the adult of mammals the remains of the second and more cephalic of the two mesal outgrowths observed in the embryo has not been identified. The caudal is the conarium. In man and very markedly in the sheep, as shown by

Wilder (55, Fig. 4711, 57, Fig. 25) there is a mesal pocket of endyma which is reflected from the supracommissure over the cephalic aspect of the conarium. Cephalad it is continuous with the endyma covering the plexuses which lie in the elongated interval between this point and the porta. Whether this sac with its cephalic extension to the porta, and its intimate relation to the large vessels and plexuses which lie dorsad of it can be identified with the paraphysis of amphibia is not known but certainly a strong resemblance to the facts in diemyctylus can be seen. As the roof of the cavities in this region is a mere membrane it does not seem improbable that a structure, in lower forms closer to the portæ, might be drawn, with the great vessels with which it is associated, to a distant point by the growth of the callosum, around the caudal end of which those great vessels effect their entrance to the brain plexuses.

Burckhardt (7, p. 398) suggests that the caudal border of the supraplexus rather than the supracommissure be considered as the boundary between the prosen-and diencephal. From the preceding studies it would appear that the opening of the paraphysis would be a more exact demarcation in the groups in which it has been identified especially if the form found in amphibia be considered from its exact definiteness, the typical condition. The embryonic form (Fig. 73) with the opening of the paraphysis in a partition between the two segments would be the point of departure, on the one hand, toward those forms in which the segments are not divided by a partition and which have no plexuses, on the other toward those in which the plexuses are well developed and the segments distinct.

In fishes this would be a convenient landmark, as in amphibia. In lamprey the part in which the left habena lies must be conceded to belong to the diencephal hence the extreme cephalic position of the part here called paraphysis need not be a bar to considering its opening as the dorsal limit between the prosen-and diencephal. Among the mammals, should the inference made above as to the paraphysis be correct, the case is more difficult because much, or perhaps all of

the long plexus between the portæ and conarium would belong to the prosencephal. The relations of the plexuses in man as shown by Wilder (55, Figs. 4743, 4711) are very different from those found in amphibia, unless some new light shall be thrown upon them by the study of sections by the microscope. Upon such a study must depend the determination of the homologies of the plexuses and consequently the dorsal limit between the segments.

The cells of the paraphysis of diemyctylus are cubical and not flattened as over the plexuses. Jeffries Wyman (59) accurately described and figured cells in the frog, which were taken from the midst of the vascular mass (supraplexus) and surmised that they were part of the brain wall proper. This is the earliest reference which I have found to this structure (the paraphysis) but it has been overlooked in the extensive bibliographies upon the epiphysis and paraphysis in which the discovery has been assigned to much later investigators.

The original use of this organ has been by some considered as an eye (19) by others (45) as an auditory organ. Another surmise may be ventured. From its origin in the embryo before the plexuses are formed, in a region, which by later growth as shown by its extensive vascular supply, has need of a means of repairing waste; from the character of the one layered endyma in the amphibia, it is suggested that it is connected, at least in early stages, with the nourishment of the brain.

SULCI.

In the mentencephal of human embryos, His (26) has very carefully worked out the relation of the origin of nerve roots to certain folds in the brain wall which become the center of cell proliferation. These arise at a margin between the solid and membranous portion of the wall (see Fig. 86, 92, which show such folds at the origin of the 9th and 7th nerves), and may be gradually overgrown by a new fold; thus pushed together, they may coalesce and apparently disappear as true folds. (See wing of cinerea with which the 10th is connected in Fig. 86). These folds he calls *Rautenlippen*. The relation of such folds with nerve roots is clearly shown by Goronowitsch (21) in

acipenser and amia. In figure 93 is a representation of the position and length of these folds as seen from the meson. It is proposed to call these depressions, *sulci*, in analogy with the term sulcus of Monro which is considered as a feature of great morphological significance, and to differentiate these endymal depressions from the *fissures* of the ectal surface. To a ridge between two sulci the term *lophius*, Gr. λόφος, ridge, is proposed. "Rautenlippe" is ill adapted to English and French, while furrow and ridge are not capable of universal application.

In man, His has recognized that one sulcus, the sulcus of Monro, has a morphological significance, indicating the boundary in the cephalic region between the dorsal and ventral zones (34). In the present investigation it has become evident that not only this and those of the metencephal but also other sulci in the cephalic parts of the brain may be looked upon as occurring at definite places with definite relations in the three forms studied. In the region of the metencephal the sulci are most clearly defined. In the larval diemyctylus the mesen-and diencephal show sulci clearly. In the adult some of these have become nearly obliterated on the endymal surface but can be clearly seen in section by the bulging of the cinerea (p. 275). In lamprey the endymal surface is not much thrown into folds and the cinerea is not clearly defined as in the diemyctylus, but from definite points the cinerea is seen to be continuous with the endyma, the cells, so to speak, streaming off in definite channels. In the amia the sulci appear, but the indefinite arrangement of the cells does not as yet help in the solution of the question.

It is hoped soon to make a comparative study of these sulci in different forms and to bring them into correlation, but certain of them are now definite enough to be used in the following discussion.

MESENCEPHAL.

The lobes of the mesencephal in the urodeles unite by a broad band and form a slight depression, at least in diemyctylus, upon the dorsimeson (Fig. 24). In fishes, reptiles, etc.,

the parts unite and a distinct commissural band is present while there is a great depression on the dorsimeson separating the parts into two lateral lobes (geminums Fig. 100). In larval diemyctylus, though the walls approximate each other, they unite across the meson merely by a layer of endymal cells (Fig. 81). In the lamprey the solid parietes show a bend, or sulcus, similar to that of the amia but the flexure is not as great, nor do the parts unite across the meson except by a wide membrane (Fig. 108). The membrane is plexiform with a mesal fold, while at the union of the membrane with the solid wall the endyma is reflected over a ridge or lophius comparable to those of the metencephal. These different forms arise from a common embryonic one where the walls are thin and uniform.

This recapitulation and comparison of figures is introduced to recall the fact, that in parts which are homologized without hesitation, the mere condition of a more or less upright position and the closer or more remote union by a well organized commissural band or a mere membrane are not considered bars to such homologizing.

PALLIUM.

Since Rabl-Rückhard's (40) memorable work on the brain of fishes, the pallium has been known as a membrane which represents and takes the place morphologically of the dorsal and mesal walls of the cerebrum of other groups. A recent work of Herrick upon the ganoids (24. p. 153), shows that he considers the portæ of other forms to be represented by the space between the proplexus [auliplexus] dividing the hemicerebrums and the floor of the prosencephal. They are elongated slits. "These changes . . . . . and the backward revolution of the mantle portion of the cerebrums make all the difficulties disappear, and we seek the commissures of the mantle far cephalad in front of the thin membranous portion, which seems to be homologous, in part at least, with the velum cerebri supporting the proplexus." Here is a hint that he has seen a new interpretation of the pallium though in other parts of the article he seems to accept in full the idea of Rabl-Rückhard.

A reconsideration of the exact relation of parts seems desirable. At its middle, the pallium extends over the cerebrum (Fig. 97) and far around to the lateral aspect. Farther cephalad it is divided by a mesal partition into two parts. The cavities so enclosed are sometimes called lateral ventricles. The partition extends caudad soon, however, ceasing to form a complete separation but hanging as a plexus into the common cavity of the prosencephal, the auliplexus. Caudad the pallium opens into the dorsal sac, paraphysis (Fig. 98). At the level of this figure it is seen to be reflected laterad over a rounded ridge which, in tracing caudad, is seen to be directly ventrad of the knob known as the habena (Fig. 99). The little sulcus *sl* is the caudal extension of the lateral pocket formed by the pallium (Fig. 98 *sl*), and the outer border of this pocket *z*, corresponds to the union of pallium and cerebrum (Fig. 97 *z*).

In the lamprey a section (Fig. 106) which cuts the habenæ as does figure 99 in amia, shows that ventrad of the habena on the left is a sulcus, on the right a membranous extension of endyma. Following these cephalad (Fig. 105) the supporting columns of the habenæ disappear and the lateral pockets of endyma extend beyond the cerebrum, while between them arises the small sac here called the paraphysis. At the side these sacs are reflected over the lip of the cerebrum. Imagine the dorsal limb of the cerebrum (Fig. 105) revolved laterad and then in their essential relations these sacs are an exact counterpart of the pallium of fishes, though the great cephalic extension of the left habena disguises the fact somewhat.

In amphibia and higher forms is it possible to recognize such a membrane? In figure 22 are seen sulci ventrad of the habenæ. These traced cephalad become the slight lateral recesses seen at each side of the opening into the paraphysis (Fig. 21, 53, 20, *pl.*). In figure 19 the membrane is divided by the intrusion of the auliplexus. Cephalad of the opening of the portæ the union of the membrane with the cerebrum is characterized by a reflection of endyma over a rounded ridge (Fig. 18, 101 *z*), at the ventral end of the mesal wall of the

cerebrum. Small as these parts are, from the exact coincidence with the essential points in the topography of the pallium of amia, I think they can be safely homologized therewith, provided that it is admitted that the mesal wall of the cerebrum in amphibia corresponds with an extreme lateral point in fishes, that is, if the points at which the membrane attaches to the cerebrum are homologous.

The figures by Mihalkovics (33) of the brain of an embryo rabbit show relations of the membranes much like those of diemyctylus.

CEREBRUM.

In figures 97, 101, 105 are shown sections through the brain of amia, diemyctylus and lamprey respectively in regions as accurately corresponding as possible,—through the cerebral commissures. In the lamprey the cavity of the prosencephal extends at right angles from the meson and the dorsal walls may easily be imagined as bent downward so that the actual condition should be as in diemyctylus, or away from the meson when the position would correspond with the interrupted lines of figure 101.

In the amia suppose that the recurved cerebrum be raised to a nearly vertical position as shown by the interrupted lines of figure 97. A strict comparison could be instituted between the forms, which would produce no more change than occurs in nature in the position of the walls of the mesencephal of different groups (p. 292). In figure 97 with the exception of stretching the line between y and y′ and folding the pallium to form a paraplexus no change except raising the parts is necessary. In the young amia (Fig. 102) as shown by Wilder (50), young gar, shown by Wright (58), lepidosteus shown by Balfour and Parker (3, Pl. 24), the walls actually have the position here imagined in the adult.

In figure 97 it is noticeable that a band of alba can be seen continuous with the commissure, passing ectally around the sharp angle at *y* to the point *z*, where the pallium unites with the solid wall. To prove that the part between *x* and *z* in this figure is identical morphologically with the corresponding

part of figure 101, that is with the callosal eminence, it is necessary to prove that fibers representing a true callosum enter this part. The researches of Herrick upon the bony fishes (25) show that callosal fibers do reach an extremely lateral position, the hippocampal lobe as he calls it, but more extended studies are necessary.

In figures 95 and 97 are seen slight undulations in the endymal surface of the cerebrum. These are continuous for some distance cephalo-caudad. In bony fishes similar undulations have been noted by Herrick (25) and given the name of fissures found in mammals upon the ectal surface of the brain and by means of them he has divided the cerebrum into lobes, despite the fact that they are upon endymal surfaces. A better explanation seems to me involved in the term sulci, to designate them; that is, definite folds in the endymal surface which have a morphological significance. Here they would indicate and correspond to the sulci so marked in the paracœles of diemyctylus at which the mesal walls bend over from the lateral wall. An illustration of the facts which seem to exist, is afforded by placing the ball of the thumbs toward each other, as much recurved as possible. This represents the amia brain, the edge of the nail the point of reflexion of the pallium, the creases at the joints the almost obliterated sulci of the cerebrum. Flexing the thumbs and placing the nails toward each other, the form of the diemyctylus brain is represented, the edge of the nail is the point at which the endyma is reflected to form the pallium and plexuses, while the sharp angles at the joints are the deep sulci occurring at the points where the brain wall changes its direction.

How exactly homologies can be established between the sulci in different groups in unknown but from the present study it is believed that the more important of these will be found to occur in similar regions of the cerebrum.

If the above interpretation of pallium, auliplexus and cerebrum receives confirmation from more extended observations, brains with recurved cerebrums cannot be said to have true portæ, the opening into the olfactory lobes representing a part only of the portæ of amphibia. The opening from the aula is

not circumscribed by homologous parts in the two types. The term paracœle however, applying to the space between the cerebrum and pallium in fishes is perfectly comparable to the paracœle of other forms.

RHINENCEPHAL.

In this article the term rhinencephal has been used as though the olfactory region might be considered a segment as independent as the prosencephal. The lack of a distinct mesal portion in higher forms has led Wilder (56 p. 114) to reject such independence.

Upon embryological grounds it seems as though the rhinencephal were equally entitled with the prosencephal to a share of the aula as a mesal cavity. In the embryo there are two portions of the forebrain—one associated with the developing olfactory nerves, the other lying next the diencephal—with a large common cavity. In the larval diemyctylus (Fig. 71), a cephalic part of the cavity belongs to the olfactory region, a caudal to the cerebrum ; the porta gives free opening of both into the aula. With the growth of the callosum and callosal eminence, the olfactory lobes are pushed away from their evident connection with the aula by that which may be called an intercalated portion of the cerebrum ; the caudal part of the cerebrum retains its original relations (Fig. 36).

The brain of the lamprey (Fig. 103), does not progress beyond the condition of the larval diemyctylus. From the porta the cavity forks, the cephalic part extending into the olfactory lobe (Fig. 104), the caudal, a short distance into the cerebrum proper (Fig. 106).

From sections of amia (Fig. 93–95) it is seen that on the ventral side it is difficult to set a caudal limit to the olfactory lobe which may extend quite to the precommissure. The prosencephal would then be represented by a wedge with a narrow base, both segments having equal share in the large aula.

In adult mammals the original conditions are masked by the great growth of the callosum and fornix but in early embryos the relations are simple and not unlike that of the

larval diemyctylus. The development of the cerebral commissures (p. 281) will undoubtedly throw further light on the question of the rhinencephal as a separate segment.

SUMMARY.

1. A true metapore exists in adult diemyctylus and indications of it appear in larvæ. In lamprey and amia at a corresponding part of the metaplexus a sac communicating with the metacœle protrudes over the myel.

2. The callosum and the callosal eminence are only beginning to develop in early larvæ of diemyctylus, and the position of the cerebral commissures differs, in early stages, more from the anurous type than does the adult, the aula being much larger proportionately. The type in urodeles and fishes may be one of an arrested embryonic development. In the diemyctylus there is evidence, in the adult, of a caudal growth of the terma which if continued would bring the commissures in the same relation to the terma as in the frog and higher forms.

3. The crista in diemyctylus and amia is shown to be a definite structure beyond which the cerebrum develops cephalad and from over which the auliplexus is reflected, and thus is a landmark in discussing the relations of the aula and cerebral commissures.

4. The paraphysis of diemyctylus is traced through different stages of development and homologies discussed in amia and lamprey, and a possible use in the nourishment of the brain is suggested.

5. Sulcus is proposed as a general term for the furrows on the endymal surface, which have a morphological significance, and lophius for the ridges between sulci.

6. In the discussion of the geminums it is shown that homologies are not dependent upon the membranous or solid condition of the roof nor the angle at which the parts unite.

7. The morphological relations of the pallium are considered in amia and its homolog in amphibia and lamprey suggested.

8. The cerebrum of amia and other fishes is not to be considered from its recurved position as different from other

types. The sulci upon its endymal surface are compared with those of diemyctylus. The pallium is considered as a plexus much stretched, not an undeveloped part representing the dorsal and mesal walls of other brains.

9. Arguments and facts are given for considering the rhinencephal as equal to other segments having a tripartite arrangement.

This investigation has been carried on in the Anatomical Laboratory of Cornell University where material and appliances were most generously placed at my disposal. To the writings of Dr. Wilder many references have been made but to his lectures especially am I indebted for the full discussion of morphological problems and especially of the difficulties involved.

ITHACA, N. Y.,
Aug. 19, 1893.

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EXPLANATION OF PLATES.

ABBREVIATIONS.

a.—aula.
ap.—auliplexus.
ar.—arachnoid.

b.—bone.
b. v.—blood vessel.

c.—cartilage.
cal.—callosum.
cb.—cerebellum.
c. e.—callosal eminence.
cer.—cerebrum.
ch.—chiasma.
cm.—cerebral commissures.
cr.—crista.

dc.—diacœle.
Dien.—diencephal.
dp.—diaplexus.
du.—dura.

e.—endyma.
ec.—epicœle.
Epen.—epencephal.
ep.—epiplexus.
epi.—epiphysis.

gl.—intermaxillary gland.
gm.—geminum.
gn.—ganglion.
gs.—gasserian ganglion.

hb.—habena.
hp.—hypoarium.
hy.—hypophysis.

inf.—infundibulum.

l.—lophius.

mc.—mesocœle.
md.—medulla.
Mesen.—mesencephal.
Meten.—metencephal.
mp.—mesoplexus.
mtc.—metacœle.
mtp.—metaplexus.
mtpr.—metapore.
mu.—mucosa.
my.—myel.
myc.—myelocœle.

n.—nostril.
nc.—notochord.

olf.—olfactory lobe.

p.—porta.
par.—paraphysis.
pc.—paracœle.
pcm.—precommissure.
pl.—pallium.
pocm.—postcommissure.
pp.—paraplexus.
pr.—preoptic recess.
Prosen.—prosencephal.
prc.—prosocœle.

rc.—rhinocœle.
Rhinen.—rhinencephal.

sc.—saccus vasculosus.
scm.—supracommissure.
sl.—sulcus.
sp.—supraplexus.
st.—striatum.
sl. cm.—Sylvian commissure.

t.—terma.
th.—thalamus.
tr.—torus.

Roman numerals I to XII indicate the cranial nerves.

GENERAL DESCRIPTION.

The general views of the brain, including the mesal aspect, are reconstructed from camera lucida drawings of transections cut through the entire head. These reconstructions were corrected, as far as possible, by comparison with camera lucida drawings of both frontal and sagittal sections through the head. The details were in all cases studied with higher magnification than was used in drawing. Some of the sections shown were cut a trifle obliquely, and were chosen because slight differences in level often exhibit transitions of form and structure which are instructive.

No attempt has been made to accurately define the limits of the five segments, because several of the questions of homology involved are still unsettled. The general arrangement of the cells is represented but with no attempt to show accurately their size. The membranes, dura arachnoid, pia, blood vessels and capillaries are usually shown at the left, the right of the brain being free. The skull, for lack of space, is not represented.

The magnification of each figure is given in the explanation.

PLATE I. FRONTISPIECE.

From photomicrographs taken by Simon H. Gage.

FIG. 1. Frontal section of the head of a large red *Diemyctylus viridescens* at the level of the portæ. × 10. It shows the brain cavities as continuous from myelocœle to rhinocœles, the extent of the cinerea, and more indistinctly the plexuses. Owing to the hardness of the lens it could not be cut and the eye was torn in its removal (cf. Fig. 35–40).

There appears a trace of the intermaxillary gland and latero-caudad of the ear a deeply stained mass the nature of which is not known but which is found in all post embryonic stages examined (cf. Fig. 40).

The angles in the cephalic cavities show the caudal limits of the rhinocœles. The portæ are wide, a horn of cinerea, probably representing Ammon's horn (p. 263) extends latero-caudad from each while directly caudad are the white masses, the dorsally directed columns of the callosum.

Between the cephalic part of the ear and the brain, the open space is part of the endolymphatic sac and the lateral recesses of the epicœle come into close contact with this sac.

FIG. 2. A similar section from a larval diemyctylus 1 cm. long. × 50. Contrast the small relative amount of alba, the membranous mesal walls of the cerebrum, the wide dia- and mesocœles, the extreme cephalic and lateral extension of the lateral recesses of the epicœle, and the fact that no trace of columns of the callosum can be seen. (cf. Fig. 69, 71). The level of the section is shown at 2 Fig. 67.

PLATE II.

FIG. 3–5. Reconstructions of brain of adult diemyctylus, male, 9 cm. long. × about 17. (cf. Pl. VI). Interrupted lines indicate the extent of the cavities; coarse dots, cinerea which appears on a natural surface. Cinerea is seen on all sides of the olfactory lobes.

FIG. 3. Ventral view. Cinerea marks out the extent of the terma, a few cells passing ventrad of the cerebral commissure to the chiasma, and is coextensive on the surface with the cavity of the infundibulum which is partly covered by the hypophysis. The ganglia at the left nearly touch. The 8th nerve is more ventral than the 7th and does not extend so far caudad. The rings on the 2d, 3d, and 4th indicate the foramens of the skull through which they pass. The geminums are scarcely visible.

FIG. 4. Dorsal view. Cinerea covers the habenæ, the tip of the infundibulum seen ventrad of the 3d, the dorsal side of the epencephal, with a mere trace at the side of the metaplexus, and at the caudal end of the geminums. The habenæ are at a lower level than the cerebrum and the relative position of supraplexus, including the paraphysis, the epiphysis and postcommissure is shown, and the metapore is indicated.

FIG. 5. In the cerebrum the relation of the paracœle to the porta and paraphysis is shown, and in the metaplexus the lateral cavities. The saccus appears caudad of the cinerea of the infundibulum. The two origins of the 1st nerve are indicated by dots in concentric lines, of the other nerves by white. The origins of the 7th and 8th are connected and a branch of the 7th passes the union dorsad of the 5th toward the gasserian ganglion.

FIG. 6. Mesal view of same. × about 29. The lines at the dorsal and ventral side with the numbers indicate corresponding figures of Plate III, the lines at the right and left, the corresponding figures of Plate IV. A portion of the intermaxillary gland is shown; the pigmented dura with folds surrounding the paraphysis and supraplexus and partially separating the hypophysis from the infundibulum; the arachnoid filling the spaces between dura and pia especially in the space between hemicerebrums; the pia with vessels extending over mesal face of the cerebrum, and interrupted with the endyma to form the metapore; the broad cut surface of the geminums; the sulci indicated by deeper shading of the cavities; the opening of the paraphysis between the auli- and diaplexus; the oblique porta; the callosum and precommissure with no cinerea intervening; and cinerea cephalad of the terma, marking the caudal progress of the latter (p. 282).

FIG. 7. A nearly mesal section from a sagittal series of adult diemyctylus' brain, hardened by Golgi's method, and showing the relations of the blood vessels with marked distinctness. × 27. Shows vessels of the supraplexus passing caudad of the paraphysis to the diaplexus; cephalad, to the auliplexus with its caudal extension into the diacœle, and also to the intercerebral pia with a loop to the crista.

FIG. 8. Transection of brain of half-grown red diemyctylus in region between 27 and 28 of Fig. 6. × 65. Shows the endolymphatic sac connecting by its duct with the ear, the blood vessels surrounding it within the dura; the mesocœle at its caudal end wider than in the adult (Fig. 26), narrower than the larva (Fig. 84); the relations of the 7th and 8th

nerve, the 7th continuous with cinerea and also receiving fibers; fibers of the 8th crossing the meson.

FIG. 9, 10. Dorsal parts of transections of the brain of adult diemyctylus, stained in carmine. × 65. Fig. 10 is caudad of 9, at the level between 23 and 24 of Fig. 6. They show the membranes passing dorsad of the epiphysis, but the vessels of the pia surround it, and do not cross the meson. The fibers of the postcommissure are mingled with fibers which apparently arise in the peculiar cells of the roof called torus. (cf. Fig. 59, 60 and p. 266).

FIG. 11. Lateral view of adult diemyctylus, male, nearly natural size, (16). *1*, the pockets at the side of the head (cf. Fig. 40).

FIG. 12. Shows length of the larva, the brain of which is represented in Plates I and VI.

PLATE III.

A few of the sections from which figures 3–6 were reconstructed. Their position is shown in figure 6 by corresponding numbers. The membranes and capillaries are shown at the left, and the position of eye, ear and nostril indicated. The cinerea is represented by dots. × about 22 (see scale).

FIG. 13. Near the tip of the olfactory lobes, showing the cells arranged in rows perpendicular to the mesal surface, the first root of the olfactory nerve I_1 and the intermaxililary gland.

FIG. 14. Through the second olfactory nerve roots I_2. Cells are continuous from ectal to ental surface.

FIG. 15. Near the boundary between olfactory lobes and cerebrum. At *olf.* are cells continuous with those belonging to the olfactory region; at *ce.* the beginning of the callosal eminence; at *t.* cells which mark the caudal path of the terma (p. 282), and are just cephalad of the portae.

FIG. 16. The paracœles are separated only by the crista and a double layer of endyma, a part of the terma. The striatum is represented by the part lying between the two lateral projections of cinerea.

FIG. 17. At the level of the portae; the hemicerebrums are united dorsally only by the pallium with its plexuses.

FIG. 18. The callosum lies between the aula and preoptic recess.

FIG. 19. Shows the lateral columns of the callosum extending to the cerebral eminence, and the auliplexus caudad of the paraplexuses. The striatum shows scattered cells connecting the two horns of cinerea. The caudal horn of the paracœle is fully established by the union of the mesal and lateral walls of the cerebrum.

FIG. 20. Through the supraplexus and optic nerves II, which extend cephalad and enter the eye at the level of figure 17.

FIG. 21. Through the opening of the paraphysis. Compare relations of thalamus and paraphysis with figure 98.

FIG. 22. Through the tip of the cerebrum containing Ammon's horn. A recess of the epiphysis expands dorsad of the habenæ while ventrad of them are the sulci continuous with *pl* of the next cephalic sections. The two plexuses appear.

FIG. 23. Through the hypophysis, infundibulum and saccus, and more cephalic portion of the endolymphatic sac.

FIG. 24. Shows the wide dorsal union of the geminums, the layers in the cinerea, and the relations of the branches of the 5th and 7th nerve as they pass to the gasserian ganglion.

FIG. 25. Shows the relation of the nerves at the level of the origin of the 5th and the lateral wing of cinerea extending to the surface of the epencephal. (cf. Fig. 82).

FIG. 26. Through the cerebellum and 4th nerve, shows the relation of the lateral recesses of the epicœle to the endolymphatic sac.

FIG. 27. Shows the cavities of the metaplexus and their relation to the endolymphatic sacs which meet near the meson.

FIG. 28. The process of a bone upon the meson is surrounded by dura and overlies a much constricted portion of the plexus, the medulla approaching the dorsimeson in the vicinity of the 10th nerve. (cf. Fig. 93 *x*). The ganglion of the 10th is partially divided, the more dorsal portion receiving the 9th nerve.

FIG. 29. Section cephalad of the metapore.

FIG. 30. At the metapore.

FIG. 31. Caudad of the metapore.

FIG. 32–33. Show the rapid flattening of the myel.

FIG. 35. From another series. Shows a dorsal union of the endolymphatic sacs, at the level of figure 27.

PLATE IV.

FIG. 35–40. Frontal sections of the brain of an adult, male, diemyctylus 7.5 cm. long, stained in haematoxylin. At the level shown by corresponding numbers in figure 6. × about 10.

FIG. 35. Dorsad of the portæ, shows the arrangement of pockets in the metaplexus (p. 267) and the change of direction in the rhino- and paracœles.

FIG. 36. Shows the relation of the cavities here interrupted by the caudal wall of the geminums.

FIG. 37. Shows the ventral dip of the rhinocœle.

FIG. 38. Shows the crista and the relative position of nerves.

FIG. 39. The nerves are a composite from three sections.

FIG. 40. Shows the base of the brain in relation of the parts of the left side, including 1, 2, 3, the pockets from the skin which develop in the adult male (Fig. 1) and receive branches of the 7th. *x* (Fig. 1) an unidentified body.

FIG. 41. An enlargement of Fig. 35. × about 60. Shows the relation of the two roots to the olfactory nerve, a branch of the 5th crossing it on its way to the intermaxillary gland; the relation of pia to the nerve roots; the continuity of ectal and ental cinerea from the tip of the rhinocœle; the scattered cells of the callosal eminence.

FIG. 42. An enlargement of the next dorsal section from Fig. 36. × 60. The ventral curve of the callosum between the two pillars is supplied from a section from another series which was thicker. Shows the relation of the intercerebral pia; the vessels of the auli- and paraplexuses; the portæ and Ammon's horn; two layers of cinerea in the thalamus.

FIG. 43. An enlargement of Fig. 37. × about 32. The nerve tract is a composite from two sections and shows a bundle from the myel giving off a few fibers to the 11th nerve, the rest continuing cephalad as the ascending solitary bundle. The relations of the 7th and 9th to the pia are shown.

FIG. 44. An enlargement of Fig. 39. × 32. Shows the origin of the 3d nerve and of fibers from the same region which unite with the 5th nerve, also the commissure of the 3d.

FIG. 45, 46, 47. Frontal sections through the ventral, middle and dorsal parts of the crista, show the fibres and loop of vessels which it contains. × 125. Near the level of figure 38.

FIG. 48, 49. Frontal sections through the crista and part of the fornix of the cat. 49, is through the larger portion of it, and 48 through the more ventral part which continues as a slight ridge from it. The direction of rows of cells is indicated by dots. A blood vessel penetrates nearly to the crista. × 6.

FIG. 50. A frontal section more ventral than Fig. 40, through the infundibulum, saccus and portion of the hypophysis to show the membranes.

PLATE V.

FIG. 51. Transection of the brain of an adult, male diemyctylus, 5.3 cm. long, stained in carmine. × 125. Near the level of 18, Fig. 6. Shows the callosum and two parts of the precommissure separated by cells; at *f*, fibers cut transversely which may represent a fornix as they can be traced cephalad of the portae; the paraphysis cephalad of its opening into the cavities; loops of capillaries penetrating even so far as the callosum; and processes from the brain substance toward the pia.

FIG. 52. A nearly median, sagittal section, of the roof of the diencephal of an adult, female diemyctylus, 10 cm. long. × 125. Shows the paraphysis; the epiphysis with a few fibers from its caudal end; the supracommissure with processes from the endymal cells extending into it; and the transition of these cells, to those of the diaplexus.

FIG. 53. An enlargement of the paraphysis and its union with the cavity as seen in Fig. 21. × 125. Shows the pigmented dura, the vessels of the supraplexus, and the endyma of the pallium.

FIG. 54. A frontal section of a large (7 cm. long) red form. × 120. From the dorsal part of the metaplexus to show the lack of continuity in endymal cells at its caudal end (cf Fig. 55).

FIG. 55. Part of a transection from an adult female, 7. 7 cm. long, corresponding in level with 30 Fig. 6, to show the metapore. × 120. The endyma is recurved and covered by a granular matter at the opening. The pia with vessels ceases, the dura is lined throughout by arachnoid cells. (cf. Fig. 30).

FIG. 56 A more caudal part of the same section as Fig. 52 to show the metapore near the meson. × 120.

FIG. 57. Transection of the medulla of a larval diemyctylus, 16 mm. long, near the level of 88 Fig. 67. × 27. Two or three cells from the endyma are lacking at the metapore (cf. Fig. 55).

FIG. 58–60. Parts of frontal sections from the same series as Fig. 35. See 60 Fig. 6. × 125. Fig. 58 shows the epiphysis cephalad of which is the cinerea of the habenæ, and caudad are blood vessels. Fig. 59 shows the paraphysis surrounded by vessels of the supraplexus, dura arachnoid and pia; the supracommissure connecting the habenæ; the postcommissure with fibers from the cells of the "torus." Fig. 60 is ventrad of 59.

FIG. 61. Part of a transection of the brain of an adult, female, diemyctylus 11.5 cm. long, from the dorsal part of the geminum (cf. Fig. 25), prepared by Golgi's method. × 120. Shows the fine filaments *x* from the brain surface extending toward the pia; cells among the filaments with processes into the alba; processes connecting with endymal cells and cells scattered in the alba, and separating the cells of the cinerea in rows. These are a few selected fibers from the mass. In some cases fine processes apparently connect the ectal and ental set of fibers.

FIG. 62. A part of a frontal section enlarged from *x* Fig. 69. × 500. Shows a blood vessel between the cerebrum and thalamus with filaments *x* extending to the vessel.

PLATE VI.

As in Plate II cinerea extending to the surface is shown by dots, upon cut edges, by cells; interrupted lines indicate extent of cavities.

FIG. 63–65. Reconstructed views of the brain of a larval diemyctylus 10 mm. long (Fig. 12), and 2–3 days after hatching. × 56.

FIG. 63. Ventral view (cf. Fig. 3), shows the great breadth of the brain in the region of the epencephal, completely hiding the mesencephal; the small hypophysis; the deeply lobed gasserian ganglion, and the separation of the ganglia of the 7th, 8th, 9th, and 10th nerves. The 6th is somewhat exaggerated in size, and a nerve is shown caudad of 12th, probably the 1st spinal.

FIG. 64. Dorsal view (cf. Fig. 4) shows the short cerebrum overhung by the habenæ; the relatively large diencephal and mesencephal; the extensive areas of cinerea; the cephalic projection of the epencephal with its membranous roof, *ep*; the caudal expansion of the mesocœle.

FIG. 65. Lateral view (cf. Fig. 5). The origin of nerves is left white; shows the comparatively ventral position of 5th and 8th, and the long axis of the porta extending cephalo-caudad with the paraphysis opening at the caudal margin.

FIG. 66. Part of a sagittal section of the head near the meson of a larval diemyctylus, 12 mm. long. × 60. Shows the relation of the paraphysis to the plexus and the commissures (cf. Fig 7[1]; the small amount of tissue between the brain and the skin and mucosa.

FIG. 67. Mesal view of same as Fig. 63. × 130. (cf. Fig. 6). Shows the large aula, the small cerebral commissures, *cal*, *pcm*; the undeveloped supraplexus; the paraphysis, pushed cephalad by the habenæ, the endymal character of the roof of the mesencephal with a more

lightly shaded portion of the geminum (*gm.*) which approaches the meson; the small cerebellum; the simple metaplexus; and the approximation of the hypophysis and notochord. The space between the medulla and pia may not be natural. The numbers refer to the corresponding figures of other plates.

FIG. 68. A more nearly mesal section of the same series as Fig. 66 to show the persistent opening of the epiphysis and its relation to the commissures. × 120. The habena is seen in face view.

FIG. 69. Frontal section of the same series as Fig. 2 at the level shown in Fig. 67. Shows the two roots of the olfactory nerve; the undifferentiated form of the rhino- and paracœles; the caudal expansion of the mesocœle.

FIG. 70. An enlargement of Fig. 69 to show the paraphysis and diaplexus. × 120.

FIG. 71. A section ventrad of Fig. 69. At *ec* the mesal cells are at a more ventral level. Shows the cephalic extension of the aula.

FIG. 72. An enlargement of the crista of Fig. 71. × 120.

FIG. 73. A transection through the head of an embryo of 12 days, to show the cephalic flexure and the position of the paraphysis. × 40.

FIG. 74. A more caudal section than Fig. 73. Shows the crista, the cavities, and the small amount of alba.

PLATE VII.

Transections of the brain of a larval diemyctylus from which Fig. 63–67 were reconstructed, at the level of the corresponding numbers of Fig. 67. × 65.

FIG. 75. Through the olfactory nerves.

FIG. 76. The section cephalad of the portæ, shows the extent of the terma, (cf. the cinerea on the mesal view at this level, Fig. 67).

FIG. 77. Shows the remnants of the double fold of terma, the more ventral of which is the crista.

FIG. 78. Shows the portæ, the plexuses, the cephalic part of the habenæ, and the tube of the paraphysis.

FIG. 79. A part of a section between Fig. 77, 78 to show the cephalic enlarged part of the paraphysis and its relation to the membranes. The dura does not extend around it as in the adult. × 150.

FIG. 80. Shows the dia- and auliplexuses and the sulcus opposite the latter which passes into the infundibulum.

FIG. 81. Shows the close approximation of the geminums at the dorsal side and the infundibulum, composed of cinerea.

FIG. 82. Shows the cephalic prolongations of the lateral recesses of the epicœle and the three parts of the gasserian ganglion.

FIG. 83. Shows the cephalic parts of the cerebellum which do not unite at this level across the meson.

FIG. 84. Shows the caudal expansion of the mesocœle, a trace of alba in the cerebellum and a few cells at the origin of the 4th nerve.

FIG. 85. Shows the origin of the 6th nerve caudad of the 8th, and what is rare at this stage of growth, several capillaries entering the brain close together.

FIG. 86. Through the 10th nerve and ganglion and a part of the sulcus from which the 9th nerve passes off.

FIG. 87. Shows the 11th nerve and *y* a bundle of fibers which can be traced for some distance in the medulla.

FIG. 88. Shows the origin of the 12th nerve.

FIG. 89. Shows the beginning of the myel and a nerve root.

FIG. 90. An enlargement of the dorsal part of Fig. 80. Shows the epiphysis and the dorsal enlargement of the diacœle ventrad of it. × 150.

FIG. 91. An enlarged section between Fig. 78 and 80, to show the supracommissure, the rudiment of the callosum, the opening of the paraphysis ventrad of the diaplexus. × 150.

FIG. 92. An enlargement of the lateral part of Fig. 84, to show the origin of the 7th and 8th nerves, and part of their ganglia, the 7th is continuous at its dorsal part, with cells of cinerea which form a "Rautenlippe" or sulcus. A blood vessel extends among the fibers of both the 7th and 8th. × 150.

PLATE VIII.

Mesal view of the brain of a small *Amia calva*, reconstructed from transections, of which Fig. 94–100 are a few. × about 6½. Mesal views by Goronowitsch (21), of Acipenser ruthenus, by Herrick (24), and Wilder (50), of lepidosteus differ somewhat from this though there is a general agreement. The pia is shown as extending from the auliplexus between the olfactory lobes, and on the dorsal part of the geminums. It is not shown on the ventral side at all. The opening into the rhinocœle is not called a porta. No union except the terma between the hemicerebrums occurs until the commissure *cm*. From the infundibulum a cavity extends cephalad (Fig. 98), and four caudad (Fig. 100). The paraphysis and epiphysis open into the cavities (Fig. 98–99) and the latter at the usual place between supra- and postcommissures. The geminums unite by a commissure which is depressed below the dorsal limit (Fig. 100), and form a caudal recess over the valvula. The metaplexus extends as a pocket over the cephalic end of the myel, *z*, in a region comparable to the metapore. At *x* the dorsal walls of the medulla nearly meet. The endymal surface is shown marked by sulci.

FIG. 94–100. Transections of same. × about 7½. The endyma is represented by a chain of cells, the cinerea by dots; the larger blood vessels penetrating the brain are shown.

FIG. 94. At the right the rhinocœle is completely circumscribed, at the left is just closed off from the sulcus *rc* of Fig. 95. The pallium extends to the extreme lateral border and by a fold on the meson forms two paracœles.

FIG. 95. The mesal fold of Fig. 94 is separated into the auliplexus and crista.

FIG. 96. An enlargement of the crista of Fig. 95. × 22. There is no enlargement of the brain at this point except by endyma. The fibers in the crista are like those in the membranes.

FIG. 97. Shows the union of hemicerebrums by the commissure *cm*. At the left are indicated the capillaries which extend as a network throughout the brain substance to the endyma. Contrast Fig. 101. At

the right interrupted lines represent the cerebrum raised to an upright position and the pallium folded to form a paraplexus *v*.

FIG. 98. Shows the infundibulum with the hypophysis surrounding the cephalic extension; the pallium passing at the right from the sulcus *sl* laterad and giving off the paraphysis, or dorsal sac, in which is embedded the epiphysis at the left of the meson.

FIG. 99. Shows the caudal projection from the paraphysis over the supracommissure and habenæ, and hence the manner in which cinerea surrounds the habena; and the sulcus ventrad of the habena which is continuous with *sl* of Fig. 98.

FIG. 100. Shows the union of the geminums and the relation of the caudal extensions from the infundibulum.

FIG. 101. A transection of the brain of a large red diemyctylus, beginning to transform. × 22. Through the precommisure, near the level of Fig. 17 but shows the hemicerebrums much divaricated as is usual with the red forms. At the right, interrupted lines indicate the position of the cerebral walls, as though raised and carrying the plexus with them (cf. Fig. 97).

FIG. 102. The outline of a transection of the brain of a young lepidosteus, at a level corresponding with Fig. 97, copied from Wilder (50). This shows that in a young ganoid the cerebral walls occupy practically the same position as indicated by the interrupted lines of Fig. 97.

Fig. 103. A view of the cephalic half of the brain of a larval lamprey, 12 cm. long, from the *morphological* meson. × about 40. From the great development of the right habena (Fig. 107) the mesal parts are pushed to the left. The epiphysis and its stalk are shown as mesal structures. The pigment shown here as black is really a brilliant white by reflected light. The supra- and postcommissures are elongated structures, the mesoplexus sends a diverticulum cephalad over the latter (Fig. 109). The rhinocœle extends cephalad, the paracœle caudad from the common opening shown as deeply shaded. The precommissure is dorsad of the porta (Fig. 104). Another band of alba at *cm*. corresponds in position (Fig. 105), with reference to the chiasma, to *cm*. of Fig. 93. The infundibulum has a cephalic and caudal prolongation, with the former is associated the hypophysis. The optic nerve extends caudad to the eye.

FIG. 104–111. Transections of the same. × 40.

FIG. 104. Through the epiphysis, its stalk, the paraphysis (p. 285) and the tip of the left habena which protrudes into it.

FIG. 105. Through the portæ, the pallium and the opening of the paraphysis. *st* indicates a possible striatum.

FIG. 106. Through the cerebrum and the habenæ, to show the relation of the pallium to the latter.

FIG. 107. Through the habenæ and supracommissure near the point where the stalk of the epiphysis opens into the diacœle.

FIG. 108. Shows the membranous roof of the mesencephal, the mesoplexus with a mesal fold and the sulcus *s* in the walls of the geminum. The large cell at *∂* forms a ridge. In this and similar ridges the large cells are arranged.

FIG. 109–110. Portions of enlarged sections through opening of the epiphysis and the postcommissure and cells of the torus.

FIG. 111. The dorsal part of a section just cephalad of the closure of the myel to show a minute sac of endyma, in the position of a metapore.

A BACTERIAL STUDY OF ACUTE CEREBRAL AND CEREBRO-SPINAL LEPTO-MENINGITIS.

HERMANN MICHAEL BIGGS.

While the infectious nature of Cerebral and Cerebro-Spinal Lepto-Meningitis has been long recognized, the character of the micro-organism or micro-organisms producing these affections has not been satisfactorily determined. The present bacterial study undertaken at periods when these diseases were prevalent in New York may throw some additional light on this question.

The facts at hand at least clearly demonstrate that a variety of pathogenic bacteria may be found in the meningeal exudate of both cerebral and cerebro-spinal meningitis, and that these bacteria are probably the important etiological factors in these diseases. The investigations thus far made do not confirm the assumption that epidemic cerebro-spinal meningitis is caused by a specific organism.

Most of the observations here detailed were made upon cases which occurred during the eight weeks ending May 1st, 1892 and the same period in 1893. During this period for the past two years meningitis in adults has been relatively frequent in New York. The observations have almost without exception been made on adults. It is also during the same period (March and April), as the vital statistics show, that the mortality is highest from acute lobar pneumonia, and it is to this disease that lepto-meningitis both cerebral and cerebro-spinal seems most closely allied in its etiology.

In this study only those cases will be considered which were characterized anatomically by an acute suppurative exudation in the pia, not caused by the tubercle bacillus.

The cases of acute cerebral and cerebro-spinal meningitis have been grouped together, because neither from an anatomical nor etiological standpoint are there sufficient grounds for separating them.

It is further the opinion of the writer that many of the cases of cerebral meningitis would prove to be of the cerebro-spinal type at the autopsy, if the spinal cord were removed and examined. In the usual routine of autopsy work, owing to the time and labor involved, the spinal cord is not removed, unless there have been some symptoms pointing to disease in the spinal canal. The operator examines the portion of the cord accessible from the cranial cavity, and in the absence of gross evidences of disease here the remainder is not removed. As a matter of experience the writer can affirm that there is not infrequently an abundant exudation in the dorsal and lumbar portions of the spinal pia, when the cervical portion is free, and when the clinical history has given no indication of the involvement of the spinal meninges.

In the present series there are eighteen cases, of which six were cases of cerebro-spinal and twelve of cerebral lepto-meningitis. In only three of the series was the meningitis secondary to traumatism or to disease of the cranial bones or soft parts about the head. Of the cerebral cases one was primary and eleven were secondary to some local or general acute infectious process. A more or less complete bacterial examination was made in seventeen of the cases.

There has been a general feeling among medical writers that acute cerebral lepto-meningitis in adults is very commonly secondary to otitis media or disease of the soft parts about the head or cranial bones. These cases do not wholly confirm this view. In only two was the inflammation of the pia secondary to an otitis media and in one probably to a scalp wound. In the other cases the disease occurred primarily or was secondary to some general infectious disease. In the twelve cases of acute cerebral lepto-meningitis, the bacterial examination gave:

In one case pure cultures of the *anthrax bacillus;*

In one case the *Bacillus coli communis;*

In one case the *B. coli communis* with *Proteus vulgaris* (the latter was probably due to a contamination).

In four cases the *Pneumo bacillus of Fraenkel;*

In two the *Streptococcus pyogenes;*

In one the *Diplococcus intracellularis meningitidis*;
In two cases a mixed infection.

Some brief notes of the clinical histories and pathological findings in the more interesting cases follow.

CASES OF CEREBRAL LEPTO-MENINGITIS.

CASE I.—*Acute Lepto Meningitis due to the Diplococcus Intracellularis Meningitidis.*

H. T., male, aet. 28, was found in a lodging house, and no history could be obtained, excepting that he had been ill for several days. On admission, he was stupid, gave his name but would answer no other questions. There were twitchings of the muscles of the face, and rigidity of the muscles of arms and neck. This rigidity of the muscles appeared as if it were partly voluntary, and the condition seemed cataleptic. When the arms were raised they remained in the position in which they were placed for some minutes. The reflexes were increased and the skin hyperaesthetic. He would not swallow any fluid, and spit it out when it was poured in his mouth. His condition did not seem to be very serious, but 36 hours after his admission his pulse began to grow rapid, his temperature rose to 103 F., the respiration increased in frequency, and 12 hours later he died.

Autopsy:—There was hyperaemia of all the abdominal and thoracic organs, and the pia covering both the convexity and the base of the brain contained an abundant fibrino-purulent exudation. Cultures made from this exudate showed the diplo-coccus intra-cellularis meningitidis of Weichselbaum.

CASE II.—*Acute Lepto-Meningitis due to the Anthrax Bacillus.*

T. H., wool-sorter, aet. 36. The history shows that about three days before admission to the hospital he noticed a pimple on the left wrist; this became vesicular, opened and a very dark areola formed around it. His arm began to swell rapidly, and became very dark in color and extremely painful. He had no chill and complained of no fever. During this time he was treated at Bellevue Out Door Dept. with

local applications. On admission the left arm was enormously swollen and showed extensive hemorrhages into the skin and subcutaneous tissue. There was a small elevated abraded point on the wrist with a hemorrhagic areola; temperature varied from 101 to 104; pain was severe. Under treatment the swelling diminished, the pain almost disappeared; he slept well and felt well and wanted to sit up. On the third day after his admission at about 3 p. m. he complained of pain and heat in his head. One hour later he became delirious, his temperature rose to 106 F. He grew rapidly worse, and died 18 hours after the appearance of the first cerebral symptoms.

Autopsy:—Arm enormously swollen, with blebs over wrist and extensive hemorrhages into skin and subcutaneous tissue. The blood everywhere in the body was completely fluid and dark colored. The spleen was very large and soft, and the other abdominal and the thoracic organs were congested. The pia mater of the brain over both the convexity and the base was studded with hemorrhages, and the meshes of the pia both in the fissures and over the convolutions were distended with sero-pus. Cultures were made from the fluid in the subcutaneous tissue from various portions of the wrist and arm, from the heart blood, the spleen, and the pial exudate on both sides of the brain. In all of the tubes inoculated from the brain, a pure culture of the anthrax bacillus developed. All of the other tubes remained sterile. The media employed and the conditions under which the cultures were made and kept after inoculation were the same. The identity of the anthrax bacillus was established by microscopical examination, by culture reaction and by inoculation of animals

Cover-glass preparations were also made from the fluid in the subcutaneous tissue of the arm, from the spleen and the blood contained in the heart cavities. No organisms were found microscopically in these situations.

It is hardly necessary to direct attention to the extraordinary character of the localization and the findings in this case, and there seems to be no satisfactory explanation to offer to account for them. The results are stated as obtained, and their accuracy vouched for.

CASE III.—*Acute Lepto-Meningitis following Typhoid Fever, due to the Bacillus Coli Communis.*

Male, laborer, aet, 27, admitted March 26, 1892. He had been feeling unwell for about three weeks previous to admission. For the first week after admission temperature ranged from 100 in the morning to 105 in the evening, and April 1st dropped to normal in the morning with only a slight evening elevation. April 9th it remained normal throughout the day. On April 12th it rose to $102\frac{5}{10}$ and remained somewhat above normal until the morning of the 18th, when it commenced to rise gradually, and on April 20th reached 105. He then began to have a low muttering delirium. During the next week the temp. ranged between $102–105\frac{5}{10}$. On April 27, 28, and 29 he had quite severe hemorrhages from the bowels and his pulse became rapid and feeble. During these and the following days the delirium continued ; neck became somewhat rigid, and he gradually grew weaker, and died on May 2d.

Autopsy:—There were found at the autopsy extensive old but unhealed typhoid ulcerations in the lower part of the ileum and an acute lepto-meningitis with a moderately abundant sero-purulent exudation over both the base and convexity of the brain. The ventricles were distended with serum containing a little fibrin and pus.

On bacteriological examination this exudation was found to contain pure cultures of the *Bacillus coli communis.*

In this case organisms (*Bacillus coli communis*) normally present in the intestinal contents had found entrance through the ulcers in the intestines into the blood or lymp currents, had made their way to the cerebral pia and set up there an acute inflammation. This is the first case recorded of a meningitis caused by this organism.

CASE IV.—*Acute Lepto-meningitis, (Otitis Media, etc.) due to a Mixed Infection.*

G. B., aet. 55, laborer, was admitted April 11, 1892. The history given was that he became unconscious while returning home from work and was brought by an ambulance to the

hospital. Temp. at time of admission $102\frac{6}{10}$, P. 76, R. 18. He soon regained consciousness, but seemed nervous and stupid. He complained of no headache nor pain in neck or extremities. There was a foetid discharge from the left ear, and his tongue was dry, brown furred and tremulous. His temp. ranged from 102–$103\frac{2}{10}$ during the next three days, pulse from 80–90, resp. 16–25. Rigidity of the neck developed on the day following his admission and gradually increased. On the second day he became stupid and difficult to arouse and seemed to have some loss of power on the left side. On April 14th he became comatose. On April 15th the temperature varied from 102–103, the respirations became rapid and superficial (30–40) and the pulse 100 to 130. Operation was advised in hope of finding a cerebral abscess and relieving pressure by evacuation of the pus. An operation was performed by Dr. J. D. Bryant. The skull was opened above and posterior to left external auditory meatus; the dura was found free from inflammatory exudate but with only slight pulsation, and the convolutions under it seemed flattened and the brain substance rather soft. An aspirating needle was passed into the lateral ventricle and about 7 ounces of slightly blood stained fluid withdrawn. Pulsation of the dura became much more marked after removal of the fluid. A small drainage tube was then inserted into the lateral ventricle, and the external wound closed. He rallied very little from the operation and died about 7 hours afterward.

Autopsy:—An abundant fibrino-purulent meningitis was found at the base. The pia of the convexity was not affected. The ventricles were much dilated with blood stained serum, and the ependyma was granular and thickened. There was a miliary tuberculosis of both lungs. The prostate contained a large abscess which had ruptured into the peritoneum and then became encapsulated. There was also extensive tubercular ulceration in the ileum.

The bacteriological examination in this case showed the presence of a mixed infection. The *Staphylococcus pyogenes aureus* was among the organisms found. Notwithstanding the extensive tuberculosis of other organs the meningitis was not of tubercular origin.

CASE V.—*Streptococcus Septicæmia, (Acute Double-Pleuritis, Pericarditis and Meningitis, Rupture of the Spleen), due to the Streptococcus Pyogenes.*

J. M., aet. 41, sailor, was admitted April 6, 1892. The history given showed that he had been suffering from cough, accompanied by an irregular type of fever with frequent chills for about two weeks previous to admission. He was markedly alcoholic when admitted; temperature 101, pulse 110, respirations 26. The following morning, T. $104\frac{8}{10}$, P. 108. Physical examination showed the presence of abundant subcrepitant and small mucous rales to be heard over both lungs, most marked over the left upper lobe. The temperature gradually rose to $105\frac{8}{10}$ at 11 p. m., P. 112, R. 30. He was delirious and unable to swallow, and his respirations were rapid and labored. Under stimulants and antipyritics the temperature dropped to $103\frac{8}{10}$ at 1 p. m., on April 8th; the rales had diminished, the respirations were easier and the delirium less marked. At 9 a. m., April 9th, Temp. $102\frac{6}{10}$ P. 102, R. 26, and nurse reported that he was much improved, the delirium had disappeared and he was able to take nourishment by mouth. At 9.45 a. m. he was seized with an attack of vomiting and partly raised himself up in bed, when he became suddenly pale fell back unconscious and died a few minutes later.

Autopsy:—A large amount of fluid and partly clotted blood was found in the peritoneal cavity. On careful search for the source of this hemorrhage, a rupture was found in the lower internal surface of the spleen about one inch and a half in length. The spleen was large, soft and contained numerous hemorrhagic infarctions. There was also an acute inflammation of the pleura on both sides, of the pericardium and of the pia of the brain attended with an abundant sero-fibrino-purulent exudation.

Bacteriological examination showed the presence of the *Streptococcus pyogenes* in pure form in the spleen and pial exudate. In the blood from the heart there were some other organisms associated with it. This was undoubtedly a case of streptococcus septicæmia, and was probably such from the beginning, although the diagnosis during the two weeks illness before admission to the hospital had been malarial fever.

The simultaneous involvement in an acute inflammation of so many of the serous membranes is of rare occurrence. Rupture of the spleen is described in most text-books as occurring in several diseases. In a rather large pathological experience, however, the writer has never seen any other instance of spontaneous rupture of the spleen.

CASES VI TO IX INCLUSIVE.—*Acute Lobar Pneumonia with Acute Cerebral Lepto-Meningitis due to the Pneumobacillus of Fraenkel.*

The cases of acute lobar pneumonia associated with secondary meningitis were four in number. The meningitis affected both the convexity and base in all the cases. In three of these, cultures made from the meningeal exudate showed the presence of the pneumo-bacillus of Fraenkel in pure form. In the fourth case, unfortunately, no bacteriological examination was made, but there is no doubt that it was quite similar to the other cases. The clinical history of these cases differs from that of pneumonia uncomplicated by meningitis only in the more pronounced character of the cerebral symptoms after the third or fourth day, *i. e.*, delirium, rigidity of the back of neck, muscular twitchings, contracted pupils, etc., and the higher average range of temperature.

Attention is also directed here to the occurrence of acute primary lepto-meningitis due to the pneumo-bacillus of Fraenkel, the lungs not being involved. This organism is more frequently found than any other, as the causative agent in cerebral and cerebro spinal meningitis.

CASES OF CEREBRO-SPINAL LEPTO-MENINGITIS.

During the period referred to, 14 cases of cerebro-spinal meningitis occurred in the writer's service in only 6 of which, however, were bacteriological examinations made. In three of these six cases, the cultures remained sterile; in one the pneumococcus of Fraenkel developed; in one the staphylococcus pyogenes; and in one there was a mixed infection.

The history in most of these cases was that commonly found in cerebro-spinal meningitis. The temperature range varied greatly; in some of the cases running uniformly low, reaching 103 rarely or not at all, and in other cases running very high, varying between 104 and 107. The pulse rate was

usually rapid before the end. Rigidity or stiffness in the back of the neck, retraction of the head, contracted pupils, delirium, coma, and incontinence of urine and faeces were uniformly present. In a small proportion of cases there was a petechial eruption on the trunk or on both trunk and extremities. Albuminuria was almost invariably present, and in one case there was also glycosuria and haematuria. There was usually hyperaesthesia of the skin and muscles, and in two cases well marked opisthotonos. Paresis or paralysis, involving small groups of muscles or those of one side, was common. The pupils were contracted, dilated, or irregular. Early there was increased sensitiveness to light, and later there was often loss of accommodation and loss of corneal reflex. There seemed to be no constant relation between the amount of exudation found after death and the severity or character of symptoms shown during life. The duration of the cases which terminated fatally varied between 36 hours and 10 or 12 days. In only one clearly defined case of cerebro-spinal meningitis did recovery take place. In this the temperature for several days ran between 104° and 106° F.

It has been rare in the writer's experience to see cases of cerebro-spinal meningitis at any other season of the year than during the spring months, and these cases are almost invariably primary and develop suddenly without any ascertainable cause.

In several of the cases in which no culture tubes were inoculated or in which those inoculated remained sterile, cover-glass preparations made from the meningeal exudate showed the presence of diplo-cocci.

Aside from the cases presented in this paper in which a bacterial examination was made, during the same period there occurred in the writer's service nearly 20 other cases of cerebral and cerebro-spinal meningitis, including several of syphilitic or tubercular origin in which there was no bacterial examination, making a total of nearly 40 cases, most of which occurred in four months of hospital service. This fact is noted to direct attention to the prevalence of meningitis at the periods referred to and to justify the following observations which have been suggested by the study of this series of cases.

1. Purulent or sero-purulent meningitis is always microbic in origin.

2. Many cases of cerebro-spinal meningitis do not differ from cerebral meningitis except in the extent of pia affected. The etiological factor may be the same.

3. Cerebro-spinal meningitis is usually primary.

4. Cerebral meningitis is usually secondary to some infectious disease, and is only occasionally primary.

5. When the disease is secondary the cause of the secondary infection may be a different organism from that producing the primary disease.

6. The following organisms have been previously found in the pial exudate in cerebral meningitis :

a. The *pneumo-bacillus* of Fraenkel.
b. The *Streptococcus pyogenes.*
c. The *Bacillus Typhosus* of Eberth.
d. The *Staphylococcus pyogenes.*
e. The *Pneumo-bacillus* of Friedlander.
f. The *Bacillus* of "*La Grippe.*"
g. The *Gonococcus.*

My observations add two more organisms :

i. The *Bacillus anthracis.*
j. The *Bacillus coli communis.*

7. The pneumo-bacillus of Fraenkel is the most frequent cause of cerebral meningitis.

8. The latter organism is a not infrequent cause of primary cerebral and cerebro-spinal meningitis, the lungs not being involved.

9. The cases of meningitis due to different organisms do not show such constant differences from each other in the symptoms presented as to make possible the clinical differentiation as to cause.

10. The amount of the exudation bears no constant relation to the severity of the symptoms.

11. It is not possible to distinguish with certainty during life, cases of acute cerebral hyperæmia with or without oedema from cases of meningitis.

5 West 58th St.,
NEW YORK CITY,
Aug. 11, 1893.

OBSERVATIONS UPON THE EROSION IN THE HYDROGRAPHIC BASIN OF THE ARKANSAS RIVER ABOVE LITTLE ROCK.

By JOHN CASPER BRANNER.

In October, 1887, I began and carried on for one year a series of observations upon the Arkansas River at Little Rock, for the purpose of determining the efficiency of that stream as an agent of erosion and transportation. These observations consisted of a series of thirty-two measurements of discharge, three hundred and sixty-five gage readings, one hundred and seventy-nine determinations of matter carried in suspension, and a similar number of determinations of matter carried in solution by the river water. These observations were so distributed as to be as comprehensive as possible, embracing all the varying conditions of weather, temperature and rainfall; when the river was rising, when it was falling, when at a standstill; when low, when high, and whenever there was any considerable change in the volume or character of the water.*

Method of Observation.†—A cross-section was carefully measured 1,200 feet above the upper bridge, a place in the river where there was least chance of any marked change occurring within the time occupied by the observations. At the place selected one bank is of rock and the other of tough clay. Floats were sent through this section at transverse intervals of twenty-five to fifty feet, and their positions as they crossed the section were located by a transit, and the time occupied in

* This paper deals only with such conditions and changes as are possible in a given section; it does not consider the effects of curves or varying depths of the channel.

† The field observations were entrusted to Assistant Chas. E. Taft, an able civil engineer of wide experience.

floating one hundred feet was noted. Wooden rods twelve feet in length were used as floats. These rods were two inches square at one end, from which they tapered the whole length of the rod to a sharp point at the other. They were weighted so as to float upright and to leave the pointed end about two feet out of the water to serve as a signal. Where the rods could not be used on account of shallow water, a surface float with a weight attached by a cord was substituted. From the data thus obtained the volume of the river was deduced. Sets of samples of the water were taken along the cross-section at the time of the velocity observation, each set being in three parts, one each from the surface, mid-depth, and three feet from the bottom. In collecting the sample from the bottom, in order to avoid taking it from the liquid mud usually present next to the bottom, the collecting apparatus was so arranged that the sample was taken three feet from the actual bed of the stream. In order to avoid the possible mingling of the water from lower depths with that above, and to insure that the samples fairly represented the part of the stream from which it was taken, an open glass tube holding one liter was used for a collecting vessel. This was so arranged as to close securely by means of two rubber balls. When a sample was to be taken, the stoppers were caught back, leaving the ends of the tube entirely unobstructed; the tube was then sunk by means of a rod, care being taken to keep its axis parallel with the current of the stream. By means of a gage the depth to which it was desired to sink it was determined. When the vessel reached the desired point, a jerk of the string released the rubber balls, which closed the ends of the tube and confined in it a representative of the part of the stream from which it was taken. The samples were always taken at the time the volume of the stream was being measured. They were placed in separate, clean bottles for examination.

In order to determine the amount of matter carried in mechanical suspension these samples were all taken to the laboratory and filtered until the water was perfectly clear; the filter containing the suspended matter was then dried, and weighed at the temperature at which it had previously been

weighed. The amount of matter in solution was determined by evaporating the filtered water. These determinations were made for every sample collected during the year—358 determinations.* A daily record was also kept of the stage of the river during the time covered by the investigation.

These observations furnish data for the approximate determination of the discharge of the Arkansas River, and of the amount of material carried by it, both in suspension and solution, past Little Rock, during the year in which the observations were made (1887–8).

Suspended Matter.—The color of the water of the Arkansas River is due to mineral matter carried in mechanical suspension. It is more or less muddy all the year round, and even at its lowest stages, when it carries least sediment, it is not quite clear. Its color is ordinarily a yellowish brown, but it sometimes becomes dark red, at which times it carries such a large amount of mechanical sediments as to render it opaque, even as seen in an ordinary test tube.

The laws of erosion and transportation naturally lead one to expect a large amount of mechanical sediments to be removed when the volume of water or discharge is greatest. If the conditions which supply sediments to the stream were constant, this would undoubtedly be true, but the conditions are not constant, and the amount of material moved depends upon the sediment-supplying conditions rather than upon the transporting power of the water.

The matter in suspension is greatest during a sudden high rise; but after the water in the stream stands at any high mark for a few days, the decrease of the amount of suspended matter it carries is very marked. This contrast is most noticeable during the winter, probably because the frosts loosen up the surface soil and leave it in a condition favorable for ready transportation. The amount of sediment carried by the river varies widely also with the same gage reading at any stage, being greater with a rising, and less with a falling river.

* The laboratory determinations were made under my personal direction by Dr. R. N. Brackett. All the care required by quantitative chemical analyses was taken with this work.

The lowest stages of the river are usually during the latter part of the summer and in the fall of the year. At such times the water becomes nearly but not quite clear. This clearness is due partly to a decrease in the volume and consequently in the velocity and carrying power of the water, and also to the large amount of common salt, lime, etc., in solution in the water, which substances tend to flocculate and precipitate the mechanical sediments. The greatest amount of mechanical sediment found in the water during the year under consideration was 225 grains to the gallon; this was on the second of May, 1888, when the river stood at seventeen feet on the gage, and shortly after protracted rains over the whole or nearly all the hydrographic basin of the Arkansas River above Little Rock. It should be added, however, that while this high water may be taken as a type of the ordinary rises, there are times when there is but little or no rise, no increase in the volume of water discharged, but a very marked increase in the amount of mechanically suspended matter. In October, 1891, occurred one of these so-called "red rises" of the Arkansas River, and although the river was quite low—marking only 3.9 feet on the gage—it carried out 761 grains of matter to the gallon, of which only 48 grains was matter in solution. Such a condition of the water is said to be due to rainfalls on the Canadian River, an affluent of the Arkansas, which runs through the "red beds" of western Indian Territory. This illustrates well the fact to which attention has already been called* that the sediments removed bear no constant relation to the discharge.

The total amount of suspended matter estimated by the above methods to have been carried down by the Arkansas in 1887–8 was 21,471,578 tons. This estimate, however, must be regarded as far short of the truth, for the method of taking the water samples has left out of account that stream of almost liquid mud and sand that is pushed along the bed of the

* Annual Report, Chief of Engineers, U. S. A., 1874, I, p. 863; 1875, I, p. 966; 1877, I, p. 433; Physics and Hydraulics of the Miss. River, 1876, p. 417.

river at all stages, but especially during high water, and which adds enormously to the amount of material daily and hourly carried out of the hydrographic basin of the Arkansas River above Little Rock.*

Character of the Sediments.—The matter in mechanical suspension in the river water is both sand and clay. Samples taken from the thread of the stream are mainly of fine sand, but samples of sediments allowed to settle in the quiet eddies of the river show that the lighter and more flocculent sediments sink to the bottom only in the quiet portions of the water.

An analysis was made of the sediments collected in six samples of river water of the 11th of April, 1888, two each from top, middle, and bottom of the stream.

ARKANSAS RIVER SEDIMENT FROM THE STREAM.†

Sand and insoluble matter, ...	85.18 per cent.
Soluble matter, ...	14.82 "

The soluble portion contained :

Iron oxide, (Fe_2O_3), ...	4.96 per cent.
Alumina, (Al_2O_3), ...	

On this occasion the river was very high, standing at 17 feet on the gage, but it had been higher by half a foot two days before.

A complete analysis was made of the sediment collected with six litres of water May 2d, 1888, when the river stood at 17 feet on the gage after a sudden rise, and while the rise was still in progress. It is as follows :

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* In the Annual Report of the Chief of Engineers, U. S. A., 1875, II, p. 478, Col. J. H. Simpson shows how sand-bars travel down-stream. See also Physics and Hydraulics of the Miss. River, by Humphreys and Abbot, 1876, p. 147.

† Analysis by Assistant Dr. Jas. Perrin Smith.

ANALYSIS OF ARKANSAS RIVER SEDIMENT.*

	Per cent.
Silica (SiO_2)	69.53
Alumina (Al_2O_3)	11.65
Iron (ferric) oxide (Fe_2O_3)	4.46
Carbonate of lime ($CaCo_3$)	6.62
Carbonate of magnesium ($MgCo_3$)	3.52
Potash (K_2O)	.66
Soda (Na_2O)	1.14
Organic and volatile matter	2.95
Total	100.58

These analyses, together with a large number of washings of the sediment, show that its chief constituent is quartz sand. There is always more or less clay in the water.

The Finer Sediments.—Experiments have already been made by other observers which show that extremely fine material held in suspension by water may be retained in suspension for an indefinite length of time.* The observations upon Arkansas River water point to the same conclusion. A glass jar one metre in length and holding six litres, was filled with turbid water taken from the river October 10th, 1887, and was allowed to stand in the Survey office until January 16th, 1888. Within four days after it was filled the water had become comparatively clear. Very fine particles continued, however, to float about in it until January 15th. That night the weather was cold enough to freeze and feathery ice crystals penetrated the whole body of the water. As soon as the room was warmed and the ice melted, the matter in suspension was found to be collected in masses resembling strings of cobwebs, in which form it clung to the sides of the jar or sank to the bottom, leaving the water perfectly clear.

Dissolved Matter.—The matter in solution bears no constant relation to the volume of water, though in a very general way

*Analysis by Assistant, Dr. J. P. Smith.

†On the subsidence of particles in liquids, by Prof. Wm. H. Brewer, Memoirs Nat. Acad. Sci., Vol. II, p. 165.

Subsidence of fine solid particles in liquids, by Carl Barus, U. S. Geological Survey, Bulletin 36, 1886.

it varies inversely with the volume of the water, and ranges from 11 to 70 grains to the U. S. gallon. This dissolved matter is principally chlorides of sodium, potassium, and magnesium, and the carbonates of lime, soda, and magnesia. At low stages of the river there is enough sodium chloride in the water to give it a decidedly brackish taste. The analyses given below represent high and low stages of the water.

ANALYSIS OF FILTERED ARKANSAS RIVER WATER.

(Sample collected December 20th, 1888, when the river stood at nine feet on the gage).

Hypothetical Combination.

		Grains per U. S. Gallon.	*Per cent. of Solids.*
Silica	(SiO_2)	.75	11.81
Chloride of sodium	(NaCl)	1.96	30.87
Chloride of potassium	(KCl)	.44	6.93
Sulphate of magnesium	($MgSO_4$)	.14	2.20
Sulphate of iron	($FeSO_4$)	.43	6.77
Sulphate of alumina	($Al_2(SO_4)_3$)	.15	2.36
Carbonate of soda	(Na_2CO_3)	1.07	16.85
Carbonate of magnesia	($MgCO_3$)	.28	4.41
Carbonate of lime	($CaCO_3$)	1.13	17.80
Total,		6.35	100.00

Found.

Silica	(SiO_2)	.75	11.83
Sulphuric acid	(SO_3)	.51	8.04
Carbonic acid	(CO_2)	1.48	23.34
Chlorine	(Cl)	1.39	21.92
Iron	(Fe)	.16	2.52
Aluminum	(Al)	.02	.32
Calcium	(Ca)	.45	7.10
Magnesium	(Mg)	.11	1.73
Potassium	(K)	.23	3.63
Sodium	(Na)	1.24	19.57
Total,		6.35	100.00

ANALYSIS OF FILTERED ARKANSAS RIVER WATER, LOW STAGE.

(Sample collected August 22d, 1888, when the river stood at 2.4 feet on the gage).

Hypothetical Combination.

		Grains per U. S. Gallon.	*Per cent. of Solids.*
Silica	(SiO_2)	.85	1.83
Chloride of sodium	(NaCl)	28.57	61.58
Chloride of potassium	(KCl)	.68	1.47
Sulphate of magnesia	($MgSO_4$)	3.92	8.45
Sulphate of lime	($CaSO_4$)	.75	1.62
Sulphate of iron	($FeSO_4$)	05	.11
Sulphate of alumina	($Al_2(SO_4)_3$)	.38	.82
Carbonate of lime	($CaCO_3$)	8.47	18.26
Total,		46.36	100.00

Found.

Silica	(SiO_2)	.85	1.83
Sulphuric acid	(SO_4)	5.90	12.73
Carbonic acid	(CO_3)	5.08	10.96
Chlorine	(Cl)	17.62	38.91
Iron	(Fe)	.02	.04
Aluminum	(Al)	.06	.13
Calcium	(Ca)	3.56	7.68
Magnesium	(Mg)	.78	1.68
Potassium	(K)	.35	.75
Sodium	(Na)	12.14	26.15
Total solid,		46.36	100.00

It will be noticed that at the low stage of water 61.57 per cent. of the dissolved matter removed is common salt, and 8 per cent. is Epsom salt.

This dissolved matter is invisible and consequently not of a kind to attract so much attention as the mechanical sediments, but the total for a day, a month, or a year, is an impressive one. The amount carried down in this form from October, 1887, to September, 1888, was 6,828,350 tons, and averaged 569,029 tons per month; during the single month of May, 1888, 1,161,160 tons were carried out in solution. When it is remembered that this material has all been dissolved from

hard rocks within the drainage basin of the Arkansas River some conception can be had of the importance of this method of land degradation.*

The relation existing between the matter in solution and that in suspension is what one would naturally expect, viz.: when the river is high there is least dissolved and most suspended matter to the gallon of water, and *vice versa*. This, however, must be regarded as a very general rule to which there are many and important exceptions. The results for the month of April, 1888, will serve as an example of these relations.

During that month eight sets of observations were made with the following results:

TABLE SHOWING THE FLUCTUATING RELATIONS OF SUSPENDED TO DISSOLVED MATTER.

Date, 1888.	Gage, ft.	Dis. cu. ft. per sec.	Grs. pr. U.S. gal.		Tons per day.		Total tons per day.
			Suspended.	Dissolved.	In Suspension.	In Solution.	
April 9.	5.75	19,608	29.41	15.41	26,619.1	13,947.7	40,666.8
" 13.	13.65	62,128	85.60	11.00	235,486.1	31,546.1	267,032.2
" 14.	16.30	92,199	122.50	13.60	519,858.9	59,880.3	579,739.2
" 16.	17.00	98,233	174.30	15.30	793,852.0	68,176.8	862,028.8
" 18.	13.35	65,512	112.60	15.70	340,517.5	47,478.9	387,996.4
" 21.	10.70	38,365	58.50	15.00	103,595.8	26,563.0	130,158.8
" 25.	6.20	17,627	45.17	43.76	36,753.1	35,605.9	102,459.0
" 28.	5.50	16,214	31.83	42.53	23,822.8	31,831.1	55,653.9

* But little attention has been given to the determination of mineral matter removed in solution from the land. The observations of hydraulic engineers to whom we are indebted for the determination of mechanical sediments, have not included the discharge of matter in solution, for the reason, no doubt, that they have had to deal practically with the mechanical sediments only.

Taking the observations for the entire year under consideration, the matter in solution is equal to about .31 of that in suspension, or a little more than one-fourth of the total amount removed. These relations, however, are not constant, as may be seen by a comparison of the totals in suspension and solution during the individual months or on individual days. In November, 1887, for example, the dissolved matter was greatly in excess of the suspended matter—more than six times as much—while on Oct. 13th, 1891, the suspended matter was more than thirteen times the matter in solution.

Attention is called to the larger percentage of silica in the water in times of freshets; 1.83 of the total at low water, and 11.81 of the total at high water.* The water at low gage readings is all spring water, or water that has passed through the rocks or soils instead of over them, while that at high readings is chiefly surface water. It seems probable, therefore, that the silica exposed over the surface of the ground is rendered more soluble by its exposure to weathering influences and to the organic acids of decaying organic matter, than is that of the unexposed rocks through and over which underground waters pass.

The Results.—The following tables are based upon gage readings for every day of the year, a complete set of velocity and discharge observations made and comprehensive samples of water collected on 32 days. From these observations interpolations were made to complete the table. The results of two independent sets of interpolations agree closely.

*Inasmuch as only one pair of analyses was made to determine this point it is possible that a generalization on this subject is not to be trusted, in any case it is desirable that other observations be made on this subject.

MATERIAL CARRIED BY THE ARKANSAS RIVER PAST LITTLE ROCK DURING THE YEAR 1887–8.

1887.	*Tons in Suspnesion.*	*Tons in Solution.*	*Tons in Suspension and Solution.*
October, . . .	377,557.2	354,171.9	731,729.1
November, . .	16,449.9	102,082.4	118,532.3
December, . .	700,558.2	444,062.5	1,144,620.7
1888.			
January, . . .	230,400.4	481,925.9	712,326.3
February, . . .	999,398.0	468,320.5	1,467,718.5
March, ...	2,391,281.0	666,753.5	3,058,034.5
April, ...	4,381,629.2	818,474.6	5,200,103.8
May, ...	6,208,717.0	1,161,160.0	7,369,877.0
June, ...	4,467,377.4	860,214.0	5,327,591.4
July, ...	296,234.2	499,869.2	796,103.4
August, ...	121,955.5	383,369.5	505,324.0
September, . .	1,280,020.6	577,946.4	1,857,967.0
	21,471,578.	6,828,350.	28,299,929.

The total bulk of this material would make a cube whose sides would be 749.2 feet in length.* The total suspended

*The specific gravity of the suspended matter is assumed to be 2.13—an assumption based upon an average of seven determinations of the specific gravity of Arkansas River sediments. It is worthy of note that six of the samples used in these determinations were taken from sediments deposited naturally along the river, and one of them was taken from the water used in making the laboratory determinations on sediments. The specific gravity here used is therefore somewhat too high.

DETERMINATIONS OF SPECIFIC GRAVITY OF ARKANSAS RIVER SEDIMENTS.

No. 1.—Sp. gr. 1.7921. Collected Nov. 13, 1888, about 40 feet east of the St. Louis, Iron Mountain, and Southern Railway bridge (upper bridge) on the north bank of the river within a few feet of the water's edge.

No. 2.—Sp. gr. 1.7764. Collected Nov. 13, 1888, about 100 feet east of the St. Louis, Iron Mountain, and Southern Railway bridge on the north bank of the river.

No. 3.—Sp. gr. 1.8043. Collected Nov. 13, 1888, about 40 feet west of the St. Louis, Iron Mountain, and Southern Railway bridge, on the north bank of the river.

No. 4.—Sp. gr. 1.8014. Collected Nov. 13, 1888, about 100 feet west

matter, if spread over the hydrographic basin of the Arkansas River above Little Rock*—140,000 square miles—would have a thickness of .000,082 of a foot; the total dissolved matter would have a thickness of .000,024 of a foot, or the total suspended and dissolved matter would be .000,106 of a foot in thickness. Erosion over this area during the year 1887–8 therefore took place at the rate of one foot in 9433 years.

The interpolations made in the observations on sediments discharged, necessarily detract from the value of the conclusions reached in regard to the quantity of material carried out of the basin. These conclusions must, therefore, be accepted only with the confidence to which the methods followed in the work entitle them. The means at the command of the Geological Survey did not permit the exhaustive observations that were desirable; indeed, that a thoroughly satisfactory set of observations should be made with the modest appropriation of a state Geological Survey is quite out of the question. The observations have some value, however, on account of their never having been made at this point† be-

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of the St. Louis, Iron Mountain, and Southern Railway bridge on the north bank of the river.

No. 5.—Sp. gr. 1.8090. Collected at the foot of Spring St. on the south bank of the river. A cube of 21.9 grams was dried at 120° C., and allowed to stand several days in the air.

No. 6.—Sp. gr. 1.17603. Collected Nov. 13, 1888, about 15 feet east of the St. Louis, Iron Mountain and Southern Railway bridge on the south bank of the river.

Nos. 1, 2, 3, 4, and 6 were air-dried.

No. 7.—Sp. gr. 2.5632. A mixture of the sediment from six bottles of water collected for sediment determinations, May 2, 1888.

The specific gravity of the dissolved matter is assigned it from the specific gravities of the constituents (in their proper proportions) found by analyzing the filtered water.

* The area of the hydrographic basin above Little Rock was kindly furnished by Henry Gannett of the U. S. Geological Survey. Other estimates make it somewhat larger.

† The investigations of Humphreys and Abbot include a series of discharge and current measurements on the Arkansas River at Napoleon. As those authors point out, however, (Physics and Hydraulics of the Miss. River, 1876, p. 33) the water of White River was included in their

fore, and it is hoped that no other apology is necessary for their publication. But whether the work had been thoroughly comprehensive or not, it is evident from the behavior of this large stream, fed from such a large and geologically diversified hydrographic basin, that slight and even local changes of meteorologic conditions may greatly change the results obtained, or those that would have been obtained, had the observations been made daily instead of occasionally. The total here given for the year 1887–8 may be twice as large or but half as large as that for the next succeeding year even with the same or nearly the same discharge of water. For this reason no estimate of results for a longer period based upon these observations or estimate for any other period of time can be more than approximately correct, because the relations of the amount of matter carried either in solution or suspension to the volume of water are not constant. A perfectly satisfactory measure of the actual work done by such a stream can only be determined by a series of observations covering a number of years, and made in connection with careful meteorologic observations during the same period over the entire hydrographic basin. It is also evident that deductions derived from observations upon the Arkansas River are not applicable to the study of other streams except in a very general way.

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measurements, although that stream can scarcely be regarded as a tributary of the Arkansas. Their results must have been considerably modified by the presence of so large a body of comparatively clear water.

PALO ALTO, CALIFORNIA,
AUG., 1893.

THE CHARACTER OF THE FLAGELLA ON THE BACILLUS CHOLERÆ SUIS (SALMON AND SMITH), BACILLUS COLI COMMUNIS (ESCHERICH), AND THE BACILLUS TYPHI ABDOMINALIS (EBERTH).

By VERANUS ALVA MOORE.

Recent study of the morphology of bacteria has demonstrated the fact which Ehrenberg had foretold, that the motile forms are possessed of flagella. The further prophecy that in these minute hair-like appendages would be found vested the power of locomotion, was partially fulfilled as early as 1875 by Dallinger and Drysdale, who saw these filaments constantly lashing on a living, moving germ (*Bacterium termo*). More recently Straus has made similar observations on several species of bacteria. Cohn, in 1872, and Koch, in 1877, stained the flagella on a few of the larger saprophytic bacteria, but the methods which they employed were so defective that for more than a decade no further knowledge was gained concerning the character or existence of these minute filaments. The recent development of staining methods by which the flagella can be demonstrated on all the motile bacteria, is therefore of considerable importance, in opening before us a hitherto unexplored field in the study of the morphology of an exceedingly large and prominent class of the Schizomycetes.

Although considerable attention has been given to the character of the flagella, the greater part of the work which has been done on this subject has been directed to the development of methods for their demonstration rather than to the filaments themselves. As a natural result of this, our present knowledge of the flagella is exceedingly fragmentary, and the few statements concerning them are, in some instances, especially with the typhoid and coli bacteria, contradictory. The

intimate relation that exists between methods and results in the study of the morphology of bacteria will undoubtedly explain many of these discrepancies. In the endeavor to bring out more fully the character of the flagella of the three species of bacteria in question, it is desirable, on account of their intimate association with the development of our knowledge of flagella, to consider first, in a general manner, the methods that have been proposed for their demonstration and to give a brief résumé of our knowledge of these filaments and their accepted significance. I furthermore wish to acknowledge my indebtedness to the various writers on this subject for many valuable suggestions.

A SUMMARY OF OUR RECORDED KNOWLEDGE OF THE FLAGELLA OF MOTILE BACTERIA. (1) METHODS FOR THEIR DEMONSTRATION. (2) THEIR CHARACTER AND SIGNIFICANCE.

Cohn[1] and Koch[3] appear to be the first who stained the flagella. The methods by which they demonstrated the existence of these filaments have not been successfully applied to the smaller and especially the parasitic organisms. Although our instruments and methods have been much improved since Dallinger[2] and Drysdale made their observations, the detection of the flagella on living, moving bacteria is a result which has rarely if ever been attained with the small and pathogenic bacteria. From 1877 to 1889 no further knowledge of these filaments appears to have been acquired.

In 1889 Loeffler[6] succeeded in formulating a method by which he could stain the flagella on a considerable number of bacteria. The process, however, was not satisfactory, and a year later he published a second method[9] which has since borne his name, and which he believed would, if properly carried out, be applicable in staining the flagella on all the motile bacteria.

A few other methods* have been proposed, but Loeffler's

* In an article[12] published in the *American Monthly Microscopical Journal*, (January, 1891), I reviewed the various methods that had been used in demonstrating the flagella on motile bacteria up to that time. See Literature, No. 5, 7, 10, and 11, at the close of this article.

has appeared to be the most trustworthy, although its application to the different species of bacteria has been attended with much difficulty. It has frequently happened, even when the method was apparently strictly adhered to, that the outcome has been absolutely negative, while in other instances the result would be entirely satisfactory.

Since the description of the original methods the literature on this subject has been exceedingly meager. In a communication to the American Society of Microscopists[13], in 1891, I pointed out several of the difficulties usually experienced in the application of Loeffler's method, and suggested certain modifications, more especially in the technique, which I had found would to a great extent overcome these objections. In the same paper it was also stated that the principle laid down by Loeffler "that an acid* producing germ required an alkaline mordant, and an alkali producing organism an acid mordant," need not be taken in a strict sense, as the flagella on certain of the acid and of the alkali producing bacteria could be stained by the use of either a neutral, acid, or alkaline mordant.

Straus[17] has recently reported a very simple method† by which he could stain the flagella on certain living bacteria. The process has given in my hands universally negative results.

Luksch[15] has modified Loeffler's method principally by

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*In 1890, Dr. Theobald Smith (*Centralblatt f. Bakteriologie u. Parasitenkunde* VIII, (1890), p. 389) pointed out the fact that liquid cultures of certain bacteria would be acid or alkaline, according as glucose or other sugars were present or absent. These undergo fermentation with the formation of acids. In liquids free from sugars the reaction remains alkaline. (See his paper in this volume.) Petruschky's (Ibid, VI, 1889) classification of bacteria as acid or alkaline producing is thus shown to depend largely on the presence or absence of carbohydrates in the culture medium.

†The method is as follows: To a hanging drop preparation of the culture a drop of staining fluid consisting of carbol fuschin one part, and distilled water three parts, is added and the preparation examined at once. He states that the moving flagella can be observed for about 15 minutes.

using a stronger solution of tannic acid in the preparation of the mordant and by the use of acetic instead of sulphuric acid in acidifying it. A very few other minor modifications of Loeffler's and other processes have been suggested, but they have in no way brought out results which entitle them to a consideration. Brown's[19] method is practically a modification of Trenkmann's process.

During the brief period of time that the existence of flagella on the smaller and especially the pathogenic bacteria has been known, two valuable applications of this knowledge have been made :

(1) *Their use as a basis for a general classification of the Schizomycetes.* Soon after the appearance of Loeffler's first method (1889) Messea*, an Italian investigator, proposed a new systematic classification* of bacteria based upon the number and arrangement of the flagella. His classification is as follows :

I. GYMNOBACTERIA (*non-motile*).
II. TRICHOBACTERIA (*motile*).
1. *Monotricha.* 3. *Amphitricha.*
2. *Lophotricha.* 4. *Peritricha.*

The *Monotricha* have one flagellum at one pole of the bacillus (*Bacillus pyocyaneus*). The *Lophotricha* have a tuft or bunch of flagella at one pole of the bacillus (*Bacillus of blue milk*). The *Amphitricha* have a flagellum at each pole (*Spirillum volutans*). The *Peritricha* are provided with rows of flagella (*Bacillus typhosus*).

* Kruse (*Centralblatt f. Bakteriologie u. Parasitenkunde*, IX, (1891), p. 107) in reviewing Messea's classification, considers it of only secondary importance. His reason for this is, that it is unnatural in that it places bacilli, spirilla, and a micrococcus together in one group (the *Monotrichia*). It does not seem necessary to consider a pioneer classification secondary merely because of an apparent inconsistency, especially in a subject about which so little is known. Undoubtedly Messea's classification was based on too limited a number of examinations, and more extended investigations will probably cause many changes to be made. At present, however, it is the only classification which incorporates the complete morphology, as known at the present time, of motile bacteria.

(2) *Their assistance in differentiating closely allied species.* Luksch[15] in differentiating *Bacillus typhi abdominalis* and *Bacillus coli communis* made use of their flagella. He found from one to three flagella on the colon bacteria, but the typhoid bacilli were endowed with from 8 to 12 filaments, a difference sufficiently great to be of differential value. He experienced much more difficulty in staining the flagella on the colon germ than on any of the other motile bacteria.

Tavel[16] has recently made the statement that *Bacillus coli communis* has no flagella* but that the typhoid bacillus is provided with them. This statement is qualified by a preceding one, that *Bacillus coli communis* is a non-motile organism, which would indicate that he was working with a different species.

In the articles, already mentioned, on the demonstration of the flagella a brief description is given of the motile appendages on the typhoid and a few other bacteria. Dallinger[4] and Zettnow[14] have discussed the flagella on a few species, more especially the saprophytic spirilla. In addition to these, there are brief mentions of the filaments on the typhoid and other species of bacteria scattered throughout the literature of the past three years, but so far as I am aware, they are too incomplete to be considered of any specific value.

THE COMPARATIVE DIFFERENTIAL VALUE OF THE FLAGELLA AND THE BIOLOGICAL PROPERTIES OF THE BACILLUS CHOLERÆ SUIS, B. COLI COMMUNIS, AND B. TYPHI ABDOMINALIS.

Bacteriology recognizes more fully, perhaps, than any other branch of biological science, functional properties in the formation of species and varieties. There are writers on this subject who consider every variation in the characters or properties of bacteria of specific or varietal significance, while there are others who hold more rigidly to the morphology of these organisms in determining their specific differences. The question, therefore, are specific differences in bacteria determined by their morphological characters or by their biological

* In 1891 I published a brief description of the flagella on the colon bacteria (Proceedings of the Am. Soc. of Microscopists, 1891).

(including etiological) properties, is one which, as yet, has no clearly defined and uniformly accepted answer. Messea's classification of motile bacteria is based on morphological characters only, and it recognizes genera, but not species. Luksch goes still further and points out a specific difference in the number of flagella of the typhoid and colon bacilli, two well recognized species of one genus. On the other hand, the more extended investigations of the biological properties of bacteria are continually bringing forth new facts, and revealing variations in the properties of these organisms which are not explained by corresponding differences in their morphology. There are bacteria which possess marked difference in their biological manifestations which resemble each other so closely in their structure that, with our present knowledge, their differentiation by purely morphological characters, is practically impossible. In the group of bacteria which includes *Bacillus choleræ suis*, *Bacillus coli communis*, and *Bacillus typhi abdominalis* we have an excellent illustration of this fact. These species resemble each other very closely morphologically but they are readily differentiated by means of their biological and etiological properties. In this group, therefore, is found a most rigid test for the differential value of the flagella.

It may be assserted that these bacteria do not belong to the same group, and while in a narrow sense (considering their more characteristic physiological manifestations only) it may be true, yet morphologically they are small, motile bacteria belonging to the *Peritricha* (Messea) and, in certain other respects, they are closely enough related to one another to be enrolled in the same genus, while their physiological and etiological properties mark their specific differences. In order that the differential importance of the biological and etiological properties of these bacteria may not be overlooked in the subsequent consideration of the specific character of their flagella, a brief summary of the more important of these properties for each of the germs in question, is appended :

(*a*). *Bacillus choleræ suis* is a small actively motile germ which is found in the organs of swine suffering from hog cholera. It

has not been found outside of the diseased animal body (or its immediate surroundings). It is *fatal* to experimental animals when injected beneath the skin in small numbers. In larger doses it will produce the disease in swine. *It ferments glucose with the formation of gas. It does not coagulate the casein in milk.*

(*b*). *Bacillus typhi abdominalis* is slightly larger than the bacillus of hog cholera and not so uniformly actively motile. It is found in the intestines and organs of people suffering from typhoid fever and is generally accepted to be its cause. Like the hog cholera bacillus, its natural habitat outside of the diseased body is not known. It is *not fatal* to experimental animals when they are inoculated with moderate doses. *It does not ferment glucose with the formation of gas*. It does not coagulate the casein in milk.*

(*c*). The *Bacillus coli communis* is a very feeble or more actively motile bacillus varying somewhat in size but usually about as large as the typhoid bacillus. It is found in the healthy intestines of both man and the lower animals. It does not appear to live in nature outside of the animal body. It is *fatal* to rabbits when they are inoculated with *large doses* of the pure culture. *It ferments glucose with the formation of gas and coagulates the casein in milk.*

Another very important feature in the study of the relation, from a differential standpoint, that exists between the biological properties and the character of the flagella of these bacteria, is the fact, which is verified by many observations, that these organisms exist in nature (*i. e.*, the coli in the healthy intestines, and the hog cholera and typhoid bacteria in the organs of the victims of their respective diseases), in variously modified forms in which the differences (biological and pathogenic) which separate the more typical species are very much diminished. This variation, especially in the pathogenic properties of the typhoid and colon bacteria, has given rise to a theory, advanced by Rodet and Roûx[16], that the typhoid germ is a modified form of the colon bacillus. In the investigation of animal diseases, hog cholera and colon bacteria have been found which varied in size and in their biological and pathogenic properties to a marked degree from

* The fact that the typhoid bacillus would not ferment glucose with the formation of gas, was first pointed out by Dr. Theobald Smith in 1890. (*Centralblatt f. Bakteriologie u. Parasitenkunde* VII, 1890. p. 502).

the more typical forms of these species.* This would indicate that the evolutionary theory of Rodet and Roûx is as applicable to the hog cholera germ as it is to the typhoid bacillus. Although the development of these specific pathogenic bacteria from a common intestinal germ is improbable, yet the possibility can not be gainsaid and the importance which this theory has in its bearing upon public health, as well as in its relation to pure bacteriology, renders its demonstration of much interest. This, and many other interesting problems connected with the specific limitations of these bacteria, emphasize the importance of determining as far as possible the extent to which their flagella may be deemed of differential value. In my efforts to do this, I have considered the flagella not only of the more typical species but also of a considerable number of modified forms (excepting the typhoid bacillus) of these bacteria. From these investigations, I have found their flagella to be much more constant than their biological properties, but contrary to Luksch, I have not found them to be of specific differential importance. The evidence to support this conclusion is found in the subsequent description of the character of the flagella.

I have limited myself to a consideration of a very few of the many interesting questions which have presented themselves in the study of the flagella of these bacteria. A large amount of experimental work was necessary before a satisfactory method for their demonstration could be formulated. This being accomplished the specific objects which I endeavored to attain are:

1. To complete as far as possible our knowledge of the morphology of each of these organisms.

*In a communication to the Biological section of the American Association for the advancement of Science, in 1890 (*New York Med. Journal* LII (1890) p. 485). Dr. Theobald Smith described a hog cholera bacillus which was, "in every way nearer the saprophytic forms (coli) than the germ usually found in epizoötics of that disease." I have found similar variations in the colon bacteria isolated from variously diseased organs of different animals. In an outbreak of swine disease in 1892, I isolated several colon bacteria which approached in their biological characters very closely to the hog cholera organism.

2. To determine whether or not there is a difference in the number or character of the flagella of the modified forms of these bacteria corresponding with the variations that are found to exist in their physiological and etiological manifestations.

3. To determine the significance of the flagella in classifying motile bacteria, as illustrated by a comparative study of these filaments on three typical species, representing morphologically three closely allied groups*, and biologically three distinct groups, of bacteria.

It was my opinion in 1891 that there was a well marked specific difference in the flagella of these species, but more extended investigations have caused me to recede somewhat from that opinion and to call attention at this time, in accordance with the results of my observations, to the similarity which exists between them.

METHOD FOR STAINING THE FLAGELLA.

The difficulties which have been experienced in the demonstration of the flagella both by myself and others, necessitate a somewhat careful consideration of the method which has been followed in obtaining the results herein recorded. As I have been unable to detect the flagella on living bacteria, my descriptions apply to stained preparations only. With the exception of certain modifications, Loeffler's method has been followed. The advantages that are claimed for the modified method over the original process are : (1) the preparations are more uniformly free from a deeply stained background which conceals entirely or renders indistinct the individual filaments ; (2) there is a better distribution of bacteria on the cover-glass ; (3) the application is more simple and the results more trustworthy. The majority of the changes which I have made were fully described in a previous article[13]. The others are incorporated here. The method as I have used it, is as follows : the principle that is involved in staining the flagella is simply the one employed in the use of a mordant or fixative. The methods which have been at all successful (beyond the experience of the originator) in staining the flagella require a

* Group is here taken in a narrow sense, signifying a species and its varieties only.

mordant which contains tannic acid. The other elements have varied. The technique of the method therefore consists in treating the cover-glass preparations of the bacteria with a mordant prior to, or together* with, the application of the staining fluid.

The mordant:†

A 20 per cent. solution of tannic acid ..... 10 cc.
A cold saturated solution of sulphate of iron ..... 5 cc.
A saturated alcoholic solution of fuchsin ..... 1 cc.

If possible chemically pure tannic acid should be used. This mordant can be used in staining the flagella of these three species of bacteria, but slightly better results appear to be obtained with the typhoid and colon bacteria when a few drops of a 10 per cent. solution of sulphuric or acetic acid are added. With the hog cholera bacteria a mordant containing a 10 per cent. solution of tannic acid gave equally good results.

The staining fluid:‡ For this I have used carbol fuchsin prepared after Ziehl's formula.

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*I have found, since the greater part of the work on this article was completed, that certain staining fluids (alcoholic solutions) could be mixed with the mordant thus eliminating their subsequent application. I have not perfected the formula for this combination but have obtained excellent results with a fluid composed of a 20 per cent. solution of tannic acid 2 cc., saturated solution of sulphate of iron 1 cc., and a saturated alcoholic solution of fuchsin 1 cc.. filter and apply in the same manner as the mordant, but for a much longer time.

†This is Loeffler's standard or neutral mordant. It is successfully employed in staining the flagella on many motile bacteria. The addition of a few drops of a 10 per cent. solution of sulphuric acid or a similar quantity of a 1 per cent. solution of sodium hydrate appears to give better results, if indeed it is not absolutely necessary, with certain other species. My personal experience tends to prove that no sharp and fixed lines can be determined for the preparation of a universal mordant. I have been unable, however, to stain a single flagellum by the use of a mordant not containing tannic acid, although I have tried nearly all of the known "fixatives." As I have stated elsewhere[13] a weaker solution of tannic acid can sometimes be used with advantage.

‡I have stained the flagella with nearly all of the basic aniline dyes ordinarily used in bacteriological work. The carbol fuchsin gives a deeper stain and consequently a clearer definition of the filaments is obtained.

Fuchsin	1 gram
Absolute alcohol	10 cc.
A 5 per cent. solution of carbolic acid	100 cc.

The fuchsin is dissolved in the alcohol, after which the acid solution is added.

The cover-glass preparations: The cover-glasses must be perfectly clean. The desired number of cover-glasses are then arranged on a level tray. A large drop of *warm* water (distilled or hydrant) is placed upon each cover-glass by means of a sterile pipette. If the cover-glass is properly cleaned* the drop of water will spread over its entire surface. The point of a cooled, flamed platinum wire is very gently touched to the surface growth of the germ on agar or gelatine and carefully immersed in the water near the center of the cover-glass. A sufficient number of bacteria will adhere to the wire to make from six to ten preparations. The tray with the cover-glasses is then placed in an incubator at a temperature of about 36° C. until the water is evaporated. Many of the bacteria on account of their power of locomotion, and by means of the currents produced in the liquid during its evaporation, will be fonnd, in the dried preparations, to be isolated from the clumps of bacteria that were introduced with the wire and distributed very evenly over a large portion of the surface of the cover-glass. This natural distribution prevents, to a marked extent, the breaking off of the flagella which occurs when the distribution is made by mechanical means in a smaller quantity of the diluent. If the water to be used

* Weber (*Fortschritte der Medicin* Bd. XI. (1893), p. 49) has found that when the percentage of calcium is too small in proportion to the alkalies (sodium and potassium) in the composition of the glass, the atmosphere will produce a chemical change in the glass which gives its surface a peculiar moist condition. This may explain to some extent the cause of the deeply stained background where the proper precautions were taken to prepare the cover-glasses. I have frequently noticed that in the use of cover-glasses that had been cleaned and exposed to the atmosphere for a considerable time prior to their use, the water would "roll up" in drops, as though the surface was covered with a film of oil, and when stained they would invariably exhibit a deeply stained background.

on the cover-glasses is heated to a temperature of about 40-45° C. and the preparations placed at once in the incubator, the bacteria are more evenly distributed.

After the preparations have dried the bacteria are fixed to the cover-glass by heat. This can be accomplished either by passing them, film upward, *twice* through the flame of a spirit lamp or Bunsen burner, or by heating them from 120°–140° C. for from five to ten minutes in a hot air chamber. The latter is to be recommended when facilities will permit.

The application of the mordant and staining fluid: In applying the mordant the preparations are completely immersed in the fluid. In place of a watch glass as formerly recommended, I have used a large (one inch) test tube for this purpose. From three to four c. c. of the mordant is placed in the tube into which the cooled, heated cover-glass preparation is dropped. The tube is held over a flame until steam is given off when it is removed. The mordant should be frequently agitated by gently shaking the tube. After from five to ten minutes the cover-glass is removed by the use of a wire hook on the end of a glass rod and with a pair of fine forceps. The cover is thoroughly rinsed in clean water, or better, in a stream from a spigot or wash bottle. If there is a grayish film on the preparation it can usually be removed by rinsing it in strong alcohol and again in water.

The staining fluid is applied in a test tube in precisely the same manner as the mordant. It is allowed to act for from one to three minutes.

The mordant should be fresh and always *filtered* before it is used. The carbol fuchsin can be kept in stock solution for a considerable time. The success of the operation depends very largely upon the *care with which it is performed.* The method as described gives excellent results with the three species of bacteria under consideration, and it has been successfully applied to a few others.*

*In the application of the method to other bacteria whose flagella will not stain by the use of a neutral solution, trials must be made with acid and alkaline mordants, and possibly with mordants containing different quantities of tannic acid, until a successful combination is found.

Cultures used: In this work, agar cultures have been employed. Unfortunately the staining method is not so applicable to preparations of bacteria from bouillon cultures on account of the presence of organic substances in the bouillon, which form a deeply stained back ground. I have, however, succeeded in making a few quite satisfactory preparations from these cultures. Gelatin and potato can be used, but with our present methods the surface of inclined agar appears to be the most satisfactory sub-stratum upon which to grow the bacteria for this purpose.

A DESCRIPTION OF THE COMMON AND MORE SPECIFIC CHARACTERS OF THE FLAGELLA ON THE BACILLUS CHOLERÆ SUIS, B. COLI COMMUNIS, AND B. TYPHI ABDOMINALIS.

In stained preparations for the exhibition of the flagella on these bacteria, there are so many variations and exceptions to what might be termed a typical presentation of the body of the germ and its motile appendages, that at present, a formula for their description can not well be written. In order to avoid repetition I shall first describe in a general way, such characters of the flagella as are common to the three species.*

The staining process necessary to bring out the flagella increases to a slight extent the size of the body of the germs. This is probably due either to the staining of a "capsular" substance which may surround the bacteria, and which is not brought out by the ordinary staining methods, or to the swelling of the cellular substance on account of the action of the mordant.†

*In this discussion the well-known morphological characters (size and form) of these bacteria are omitted. The rod-shaped forms will be spoken of as the body of the germ wherever it is necessary to distinguish between it and the flagella. The terms motile appendages, and filaments are used synonymously with flagella.

†Zettnow[14] holds with Klebs and Bütschli, that the part of the germ which is easily brought out by the ordinary staining methods is the nucleus only, and that the additional part which is demonstrated by the use of Lœffler's method is a plasma which surrounds the nucleus. Wahrlich (Article reviewed in *Centralblatt f. Bakteriologie u. Parasitenkunde* XI, (1892) p. 49) found two substances in bacteria cells, (1) the basis, a substance which gave the micro-chemical reaction of linen, and (2) a *chromatine* substance or nucleus which is contained within the meshes of the basis.

In the microscopical examination of well-executed preparations for exhibiting the flagella three conditions have been universally observed: (1) In certain fields there were a greater or less number of bacteria which exhibited no flagella; (2) there were a considerable number of detatched or free flagella lying between the bacteria; and (3) the numbers of flagella on the different bacilli were not constant. On the other hand, however, fields could be selected in which there were no detatched filaments and where every germ was provided with motile appendages.

The flagella appear as hair-like appendages or filaments, which radiate from the bacteria. They are given off from the cell wall of the germs of which they appear to be continuations or projections. This can be clearly shown by their reaction to the following staining fluid. If to 3 c. c. of the mordant 1 c. c. of a saturated alcoholic solution of fuchsin is added and the preparation treated in the usual way with this solution for about five minutes, the flagella and periphery of the bacteria will be stained with equal intensity, while the central portion of the cells will remain unstained. By allowing the reagent to act for a much longer time or by applying the usual stain, the entire organism will become deeply tinted. This would indicate that the cell wall and flagella were alike in their composition, or at least in their reaction to a certain staining fluid, and that the contents or nucleus was different. The sharp outlines of the flagella as observed in stained preparations, would indicate that they are organized elements. I have been unable to make out any differentiation of their structure.

The appearance of shorter and longer free flagella and the difference in the length of those still attached to the body of the germs is due apparently to their detachment and breaking during the separation of the individual bacteria from the closely packed masses in which they grow on solid media. In these cultures the long filaments on the different individuals appear to become entangled with each other, causing the separation of the bacteria to be accomplished with difficulty and presumably with more or less injury to their organs of

locomotion. This is suggested by watching the clumps of bacteria in a hanging-drop preparation. The germs at the edge of these masses, when about to separate themselves from the others, exhibit first a trembling motion, then a jerking, reeling and pitching movement, until finally they are free* and move across the field.

Furthermore, in the examination of a hanging drop preparation made from a bouillon culture the bacteria are observed to move much closer to each other than the length of their flagella, and it seems highly probable that detachment or breaking of the appendages is produced during these voluntary movements, by their contact and possible entanglement with each other. Free flagella have been found to be numerous in stained preparations made from liquid cultures. For the ultimate settlement of these questions a method must be devised by which the motile appendages can be observed on the living and moving germs. At present we are forced to be content with the study of the appearances that are presented in stained specimens, presuming that as the conditions of preparation are the same the characters that are revealed will be correspondingly similar in the different species.

The length of the flagella as seen in stained preparations varies to a marked degree. The longest I have measured was 18 μ or about nine times the length of the body of the bacillus (hog cholera).

The diameter of the flagella varies in different preparations and frequently in the same specimens, to a marked degree. In a deeply stained preparation they are occasionally 0.4 μ in diameter, or about one-third of the diameter of the body of the germ. More commonly they are about 0.2 μ in diameter, or about one-sixth the thickness of the organism. Again they may appear as extremely delicate lines, so fine that it is with difficulty that they can be seen at all. Usually, however, they are about 0.2 μ in diameter. The unexpected appearance of these variations has thus far baffled an explanation,

* It is an observable fact that the character of the movement of the individual germs is somewhat varied. This may be due to the loss of certain of their motile appendages.

although many series of preparations have been carefully made to discover the cause. I believe, however, that the failure is due to the technique rather than to a variation in the filaments. The diameter of the flagella is appreciably the same at the distal end as at the union with the body of the germ. Occasionally, however, the distal portion appears to be very slightly tapering.

Among the free flagella is sometimes observed what appears to be a strand or bunch of twisted filaments, varying from one to two μ in width, which presents a uniformly, deeply stained appearance. At one or both ends the filaments are separated from each other, giving the appearance of the frayed end of a cord. In preparations from old cultures several flagella which radiate from the same point are frequently observed. They present the appearance of the filaments of a single germ. These are occasionally observed in preparations from young cultures.

Frequently a flagellum will present throughout the greater part of its length a very close, wavy condition. There are in addition to these many other anomalous appearances which have as yet no clearly defined significance.

In the study and comparison of the flagella, I have employed cultures varying in age from sixteen hours to three days. There appeared to be no difference in the character of the flagella on the bacteria in cultures of these ages, but in preparations made from those of a longer growth there was usually a much larger number of broken and detached filaments.

The exact arrangement of the flagella on the body of the germ is hard to determine. In stained preparations the organisms are dried to the cover-glass with the filaments in such positions that they seem to radiate from the outer edges of the germs as they appear in the stained specimen. Frequently they all appear to come from a very small arc on the circumference. This is undoubtedly due to our inability to detect the filaments as they cross the body of the germ. The flagella are given off from both extremities, and at variable points along the intervening portion of the body of the germ,

although a single bacillus which exhibits this uniform radiation of motile appendages is rarely observed in stained preparations. The flagella are usually more or less wavy, and it is the rule, though it has many exceptions, that the waves in a single flagellum are uniform.

I have studied very carefully the flagella on several hog cholera bacteria. These were obtained from different sources (outbreaks of hog cholera) and a few of them exhibited slight variations in their biological characters and more marked difference in their virulence. So great have been these variations in a few cases that the bacteria have been deemed modified forms. I have also studied a larger number (about 20) of colon bacteria isolated from variously diseased organs of different animals and from the human intestine. These have also shown a marked difference in their properties. The two cultures more specifically described represent (1) the more typical form (2) a somewhat modified form. Of the typhoid bacteria, only two cultures have been at my disposal. All of these bacteria have been carefully studied and their identification clearly established. In these examinations I have been unable to detect any constant, specific difference in the character of the flagella on the germs from the different cultures of the same species. On this account bacteria from only two cultures of each species will be considered in the more specific description of the flagella.

The flagella on Bacillus choleræ suis. (Plate 1, Fig. 1.) (1) A culture of hog cholera bacteria which was obtained from a pig that died in an outbreak of hog cholera in the State of Illinois in the fall of 1891. An examination of the bacteria in a hanging drop preparation showed them to be universally actively motile. They were virulent.

The number of flagella on the different germs, as observed in the stained preparations, was variable. The most usual number was from two to five. A few germs have been found upon which nine filaments could be counted, but it is the exception to find more than eight. Frequently the filaments are bent upon themselves in such a way that it is very difficult to determine the exact number, especially when it is large. In

a few instances I have thought it possible for as many as twelve filaments to be present. In order to estimate the most usual number an actual count of the flagella on a large number of germs was made. These were taken from somewhat ideal fields on a considerable number of preparations. In these fields there were from 2 to 10 bacteria which were well separated* from each other and on each of which all of the flagella could be counted; that is, there were no clumps of bacteria present. Care was always taken to avoid extreme conditions.

Of these the number of flagella on two hundred individual germs was as follows, 12 had no flagella, 23 had one, 30 had two, 47 had three, 39 had four, 22 had five, 12 had six, 8 had seven, 5 had eight and 2 had nine. In many of the fields there were no free filaments, while in others there was a variable number.

The longest flagellum that I measured was 18μ.† The usual length was from 7 to 12μ. Shorter ones were quite common. Occasionally the ends of the filaments were curved into nearly or quite perfect circles or rings with a diameter of about 1.5 μ. These were not uniformly present but in occasional preparations they were quite conspicuous.

(2) A culture obtained from an outbreak of hog cholera in the State of Maryland. A microscopical examination of a hanging drop preparation showed the bacteria to be actively motile. They were less virulent than those in the previous culture. Cover-glass preparations treated and stained as in the preceding case revealed no appreciable difference in their staining properties, the number, arrangement, and character

*This is very important, for the tendency of the bacteria to be united in twos or small clumps which might easily be mistaken for a single germ is very marked, and the flagella which belong to two germs could be readily considered as those of a single individual. This is especially true where the bacilli are united end to end.

†In measuring the length of the flagella the distance from the body of the germ to the distal end of the filament along its general course was taken, without allowance for the minute curves or waves which would in some instances, if considered, add an appreciable amount to the recorded length.

of their flagella. To complete the comparison the number of flagella on 200 germs is recorded. Of these, 10 had no flagella, 33 had one, 33 had two, 45 had three, 38 had four, 19 had five, 6 had six, 8 had seven, 6 had eight; and 2 had nine. The longest flagellum observed measured 11 μ. The usual (about 75 per cent.) length was from 6 to 8 μ. The small circles at the distal ends were also present but in small numbers.

Flagella on Bacillus coli communis. (Plate 1, Fig. 2). A culture of the bacillus coli communis, obtained by Dr. Theobald Smith from the human intestine. A microscopical examination of a hanging drop preparation from an agar culture of this species showed comparatively few of the germs to be in motion. Upon watching it carefully for several minutes, many of the individual germs which were first at rest exhibited an active motility.

The diameter and arrangement of the flagella on this species do not differ to any appreciable degree from those on the hog cholera bacteria. The number of filaments on the individual germs varied considerably. Seven was the maximum number found on a single organism. As before, an actual count of the flagella on 200 individual germs selected from representative fields was made. Of these, 9 exhibited no motile appendages, 33 had one, 58 had two, 44 had three, 34 had four, 15 had five, 4 had six and 3 had seven. The number of the free flagella in many of the fields averaged about one to each germ. This is unimportant as in other parts of the preparations the number was greater and in still others less. The length of the filaments varied from 2 to 12 μ. The greatest number (66 per cent. of a large number measured) were from 5 to 7 μ. It is of interest to note that the number of individual bacteria which exhibited no flagella was no larger in this species than in the preparations of the hog cholera bacteria where apparently every germ was actively motile. A very few of the flagella formed nearly or quite perfect circles or rings at their distal ends. Their existence, even in small numbers eliminates their specific value when compared with hog cholera and typhoid bacteria.

(2). A culture *Bacillus coli communis* obtained from the pectoral muscle of a pig which died in an outbreak of swine disease in 1892. The motility of the bacteria in this culture was less marked than in those from the previous culture. The flagella extended out from the body of the bacteria in delicate, more or less wavy filaments. In diameter, course, and general appearance they differed in no perceptible manner from the flagella on the previously described germ. The maximum number of filaments that was found on an individual was one less than in the previous case, and the number which possessed but one flagellum was proportionally larger. The number of detached filaments was not in excess of those in the preparations of the colon bacteria from the human intestine. In order to arrive at a more accurate comparison, the flagella on 200 individual bacteria from selected fields were counted. Of these, 11 showed no flagella, 83 had one, 55 had two, 29 had three, 13 had four, 6 had five, and 3 had six. The maximum length of the filaments measured was 15 μ. The length of the greatest number varied from 5 to 9 μ.

Flagella on Bacillus typhi abdominalis.—(Plate I, Fig. 3). For my cultures of typhoid bacilli I am indebted to Dr. Theobald Smith. These cultures were from two to four years old. Unfortunately I have no knowledge of the history of these cultures prior to their arrival in our laboratory. (1) A culture obtained from the Johns Hopkins Hospital, Baltimore, Md. When examined in a fresh condition (hanging drop) the majority of the bacilli were observed to be in active motion.

The arrangement of their flagella was not perceptibly different from those on the hog cholera and colon bacteria. In the examination of different preparations of this bacillus a considerable variation was found to exist in the appearance of its flagella. A certain number of the bacilli were provided with long, nearly straight or wavy filaments which extended in various directions from the body of the germs, while the motile appendages on the greater number of the organisms were shorter, more curved, and intertwining, presenting a

somewhat bushy appearance about the body of the germs. In many specimens there was an exceedingly large number of flagella which were bent at their distal ends, if attached to the germ, into nearly or quite perfect circles or rings varying from 1.2 to 2 μ in diameter, while other filaments were curved to such an extent that the free ends passed either above or below the body of the germ. In many preparations I have found fields in which one or more of the filaments on nearly every germ exhibited these circles or rings. Their formation is somewhat curious and their significance is as yet speculative. Frequently many of the "rings" are broken from the flagella. The filaments were usuallly bent at right angles to their course at the point where the curve begins. This gave them the appearance of the ends of certain screw hooks. Less frequently the rings were formed by the distal part of the filaments bending to one side, forming perfect or nearly complete circles. In some preparations a considerable number of bacilli were observed around which were from one to four rings or inbending filaments with few, if any, extended flagella. The terminal rings and incurved flagella on the typhoid bacilli were very marked, but their differential value is destroyed by the fact that they occasionally appeared in preparations of the other bacteria.

The detached filaments vary in number, as in the case of the previously described organisms. The number of flagella on the individual germs also varied; ten was the maximum number that I was able positively to determine on a single germ; Luksch found twelve; and according to Sternberg[20], Babes found as many as twenty on a single germ. In the photographs of typhoid bacillus published by Fraenkel and Pfeiffer[21], and Migula[22], showing their flagella, ten is the largest number positively represented as belonging to a single germ. In these photographs, clumps and pairs of bacilli show a much larger number. A count of the flagella on 200 germs in well selected fields showed 9 bacilli to be without motile appendages, 23 had one, 39 had two, 45 had three, 27 had four, 15 had five, 23 had six, 11 had seven, 3 had eight, 3 had nine, and 2 had ten. The length of the filaments

varied considerably. The maximum length of those measured was 11 μ; 78 per cent. of a large number that were measured varied in length from 3 to 6 μ.

(2). A culture which was obtained from Koch's Laboratory (Germany). The bacteria were not quite so actively motile as the hog cholera germs. They stained readily and the flagella differed in no appreciable manner from those on the bacteria from culture (1). There were a large number of short flagella and rings. The number of flagella on the individual germs was estimated in the manner heretofore described. Seventeen of the 200 germs exhibited no flagella, 43 had one, 42 had two, 45 had three, 24 had four, 18 had five, 5 had six, 3 had seven, and 3 had eight. It is possible that a few bacteria had nine filaments each, but there was a doubt as to the exactness of the count. The longest filament measured was 13 μ. A large majority of those measured varied from 3 to 7 μ in length.

From the detailed descriptions of the flagella on these three species of bacteria a few comparisons may be made. These can be stated best in tabulated form :

A COMPARISON OF THE NUMBER OF FLAGELLA ON THE INDIVIDUAL GERMS.

Bacillus.	Culture	The Number of Flagella.										Total number of bacteria.	Average number of flagella on each germ
		0	1	2	3	4	5	6	7	8	9		
Cholerae suis .	(1)	12	23	30	47	39	22	12	8	5	2	200	3.3
" "	(2)	10	33	33	45	38	19	6	8	6	2	200	3.1
Coli communis	(1)	9	33	58	44	34	15	4	3			200	2.6
" "	(2)	11	83	55	29	13	6	3	(?)			200	1.8
Typhi abdominalis	(1)	9	23	39	45	27	15	23	11	3	3	200	3.5
" "	(2)	17	43	42	45	24	18	5	3	3	3	200	2.6

In comparing the figures in the tables the fact should be kept clearly in mind that they have only a relative significance. The large number of preparations examined and the number of counts and measurements made give them,

A COMPARISON OF THE LENGTH, DIAMETER AND CHARACTER OF THE FLAGELLA.

Bacillus.	Culture	Length of longest flagellum.	Lgth. of 70 per ct or more of the flagella.	Usual diameter of flagella.	Appearance of flagella.
Cholerae suis	(1)	18 μ	7–12 μ	0.1–0.2 μ	Usually extended, wavy, few terminal rings.
" "	(2)	11 μ	6–8 μ	0.1–0.2 μ	" " "
Coli communis	(1)	12 μ	5–7 μ	0.1–0.2 μ	" " "
" "	(2)	15 μ	5–9 μ	0.1–0.2 μ	" " "
Typhi-abdominalis . . .	(1)	11 μ	3–6 μ	0.1–0.2 μ	Many incurved, wavy, large number of terminal rings.
" "	(2)	13 μ	3–7 μ	0.1–0.2 μ	" " "

however, a good representative value. To illustrate this point and to show how easily different results could be obtained, especially in reference to the number of flagella, by considering a smaller or possibly larger number of bacteria, I have appended the results of the count of the flagella of 200 individual germs. Here also a further difference of opinion as to the fields to be selected might vary the final result. My counts in this case were made from eight preparations.

Bacillus Cholerae Suis.	Number of fields examined.	Number of Flagella.										Total number of bacteria.	Aver. number of bacteria in a field.
		0	1	2	3	4	5	6	7	8	9		
Preparation I.	5		3	6	2	8	7	1	2			32	6.4
" II.	4	2	1	5	7	5	2	4	1	2	1	30	7.5
" III.	6	1	1	2	10	6	1	3	1	3	1	29	4.8
" IV.	3	2	2	1	8	1						14	4.6
" V.	8	2	6	8	6	5	5	1				35	4.3
" VI.	7	2	3	2	6	4	1	1	1			20	2.8
" VII.	3	1	5	3	7	7	3		1			27	9
" VIII.	2	2	2	2	1	3	3	2	1			15	7.5
		12	23	30	47	39	22	12	8	5	2	200	

In comparing the specific characters of the flagella of the three species, it will be observed that while there are manifest

differences there are likewise striking resemblances. A few of the more important facts which have been brought out in this study to illustrate their differences and similarities are appended.

Their difference is shown from the observation, (1) that the length of the greater number of the flagella is greatest on the hog cholera and least on the typhoid bacilli, while those of the colon bacteria are of intermediate length; (2), that the average number of flagella on the colon bacteria is less than that on either of the other species; and (3), that the terminal and free rings are much more numerous in the preparations of the typhoid bacillus than in those of the other bacteria. This is also true of the incurving flagella.

Their similarity is illustrated by the fact (1), that the numbers of flagella on the individual bacteria vary in the different fields in the preparations from the same species as much as in those from different species, excepting in the maximum numbers; this is also true of the length of the flagella; (2), that the diameter of the flagella on the three species is identical; (3), that the position of the flagella on the body of the germ is the same; and (4), that fields could be selected in preparations from the three species in which no difference could be detected in the character of the flagella.

CONCLUSIONS.

The foregoing examinations and the results of a careful comparative study of the flagella of these three species of bacteria appear to sustain the following conclusions:

1. These three species of bacteria belong to the *Peritricha* (Messea).

2. There are apparently slight differences in their flagella, but the differences are not marked enough to be deemed of differential value. This is evidenced by the fact that the flagella in different preparations from the same species exhibit quite as marked variations.

3. There is no difference in the flagella of modified forms of the same species to correspond with the difference in their physiological and etiological manifestations.

4. Until further facts are determined, the character of the flagella will not furnish a means for specific differentiation. The species and varieties must be determined by their physiological and pathogenic properties while the genera may be fixed by the character of the flagella.

5. The proposition that the *Bacillus typhi abdominalis* is a modified form of *Bacillus coli communis* cannot be justly refuted on their morphological characters. The similarity in the structure (as it is now understood) of these bacteria increases the importance, from a differential standpoint, of the differences found to exist in their biological and etiological manifestations.

WASHINGTON, D. C.,
July 31, 1893.

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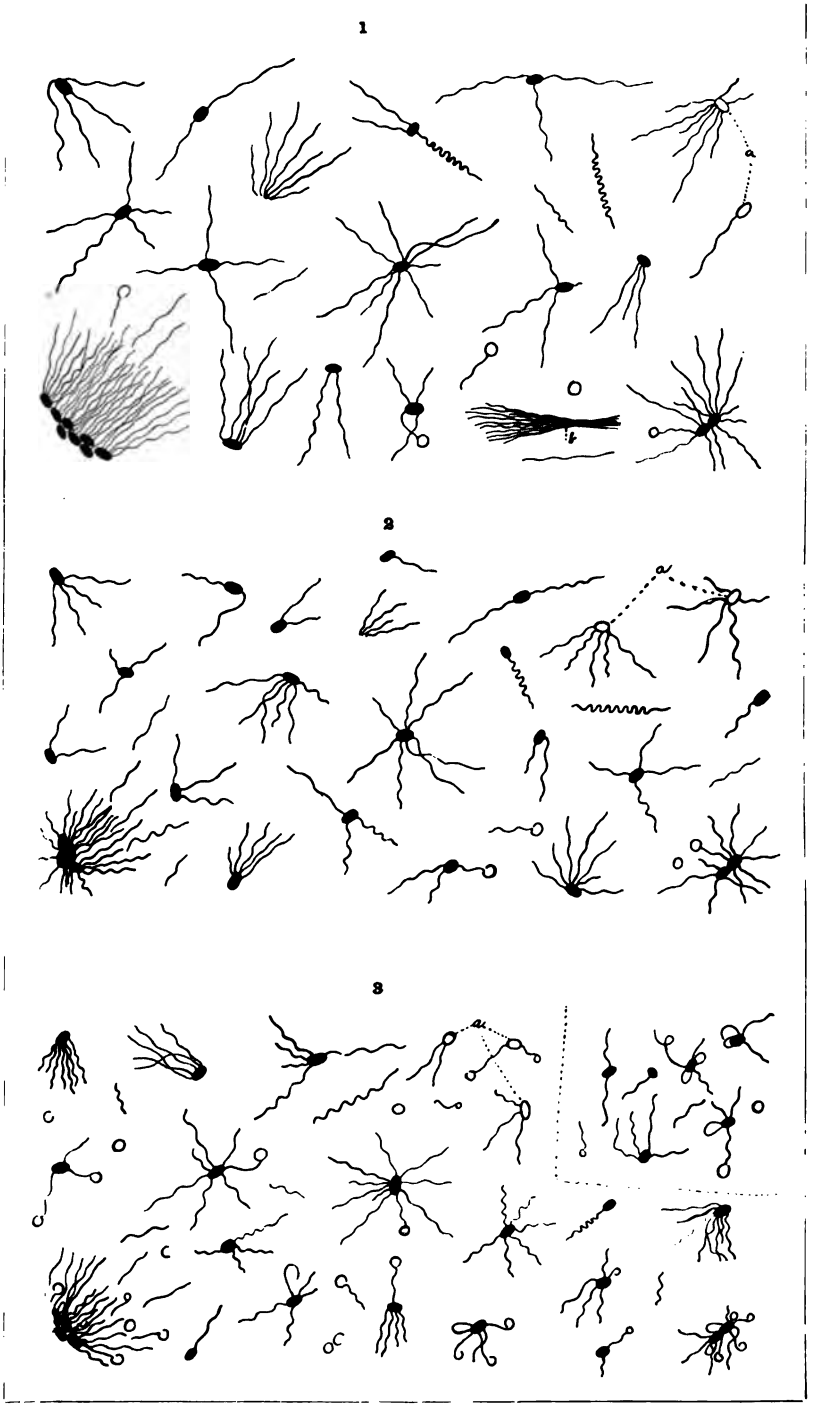
DESCRIPTION OF PLATE.

The figures in the plate are to illustrate the flagella on these three species of bacteria as they appeared in stained cover-glass preparations. The drawings were made by the aid of a Zeiss apochromatic objective, 2 mm., 1.30 n. a. and the measurements were made with the compensating micrometer ocular No. 6. Each germ and its flagella were carefully measured and in the drawings each micromillimetre is represented by a millimeter, thus giving a magnification of a thousand diameters. The curves in the flagella were carefully counted and reproduced as accurately as it was possible by freehand drawing. The position of the flagella was also carefully determined. In the preparation of the plate care has been taken to avoid extremes. Individual bacteria have been selected from different fields to represent the various number, lengths and position of the filaments on the body of the germs as they appeared in the preparations. A few free, or detached flagella are also indicated. The drawing of each germ is practically equivalent to a photograph. It is possible to find all of the structures represented in a few fields of the microscope in a well executed preparation. The germ in the center of each figure represents the maximum number of flagella on a single individual. In the left lower corner of each is a drawing of a clump of bacteria with their flagella. There are a few drawings of bacteria (*a*) with only their periphery and flagella stained.

Fig. 1. *Bacillus choleræ suis.* Drawings made from preparations of the culture of hog cholera bacteria obtained in the State of Illinois. (*b*) A bunch or strand of flagella.

Fig. 2. *Bacillus coli communis.* Drawings made from preparations from the culture obtained from the human intestine.

Fig. 3. *Bacillus typhi abdominalis.* Drawings made from preparations of the typhoid bacillus which was obtained from the Johns Hopkins Hospital. The upper right hand corner, enclosed in dotted lines, represents all of the bacteria and flagella from a single microscopic field.



FLAGELLA OF BACTERIA—MOORE.

THE LYMPHATICS AND ENTERIC EPITHELIUM OF AMIA CALVA.

GRANT SHERMAN HOPKINS.

The comparatively small number of investigations upon the lymphatic system of Fishes and Fish-like Vertebrates appears the more remarkable when we consider the capaciousness and the undoubted importance of this great vasiform system.

A possible explanation for this lack of attention on the part of zoologists may be found in the difficulties attendant on any investigation of these vessels owing to the transparency and delicacy of their walls and the liability of confusing them with the veins. To whom is due the credit of having first discovered the lymphatic system in fishes, we will not attempt to decide. Hewson and Monro both claimed the honor, but it is pretty well established that the lacteals of a fish were observed more than a century before by Bartholin* (2) though his description was alloyed with the old error that they terminated in the liver. It is doubtless true, as remarked by Abernethy that "all our knowledge of the absorbing vessels has been obtained by fragments, and that our future acquisitions must be made in the same manner." It must be allowed, however, that the lymphatic system of the lower vertebrates, especially the osseous fishes, was more completely exhibited by Hewson (8) than by any of his predecessors or contemporaries.

Hewson's three papers on the lymphatic system in birds, amphibia and fishes, appeared in the Philosophical Transaction for 1768–69. In the paper on fishes he gives a description of the lymphatic vessels in the Haddock together with some of the more striking pecularities of this system in

* See References.

fishes, among which are the absence of lymphatic glands and the incomplete development or entire absence of valves within the lymphatic vessels. According to Robin (17) Monro was the first anatomist to investigate the lymphatic system of selachians. But many of his statements are incorrect as in several instances he mistook veins for lymphatics. It was a mistake of this kind that led him to believe that the lymphatic vessels commenced by free extremities provided with small orifices. He saw the injected material ooze out upon the surface of the skin and enteric mucosa without extravasation into the underlying connective tissue and concluded that they commenced by these free openings. The general arrangement of the large lymphatic vessels in fishes, as given by Milne-Edwards (12) corresponds with the statements of most anatomists who have written upon this subject. He divides the system into two portions, one belonging to the abdominal viscera, the other to the skin, muscles and neighboring parts. Concerning the latter he says, "the subcutaneous lymphatic system constitutes, in general, three principal trunks which have a longitudinal direction, and which are situated, one on the ventri-meson, the two others on the sides, in the groove which separates the muscular masses of the dorsal and ventral portions of the body, and which can be recognized, externally, because it corresponds in position to the lateral line. This system of vessels receives a multitude of secondary branches which ramify under the skin, and it opens into the veins at its two extremities, *i. e.*, near the base of the cranium and at the base of the caudal fin." At the caudal end each lateral lymph vessel terminates in a sinus; these sinuses communicate not only with the caudal vein but with each other as well.

The investigations of Hyrtl (9) upon the cephalic and caudal sinuses of fishes, and the lateral vessels with which they are connected, led him to the conclusion that these vessels formed no part of the blood-vascular system but were lymphatics. He examined the fluid of the caudal sinus and found it "clear as water, having the same properties as the liquid contained in the lymphatic vessels of other parts of the body."

In contradistinction to the statements of the authors above mentioned, Robin says "I have satisfied myself by numerous observations and experiments, that the cutaneous and subcutaneous vessels described by Monro, Hewson, Hyrtl, etc., as lymphatics, are veins. . . . . The division of the lymphatics of fishes into superficial and deep or visceral, still adopted by some modern authors, must consequently be abandoned. The first of these classes of vessels does not exist in this class of vertebrates." As the conclusion to his article Robin further says, "the general result of these researches has been to demonstrate that the subcutaneous vessels which I have described in the selachians. . . . . as being lymphatics, are veins and not lymphatics at all. This conclusion is found entirely confirmed by the descriptions contained in this memoir; they prove, indeed, that fishes have no other lymphatics than the chylous vessels, and those of the peritoneum lining the genito-urinary organs and the pericardium."

So far as I have been able to ascertain, no other writer shares this opinion. Indeed from the statements of various authors and from my own observations, I think Robin was wrong in calling the subcutaneous vessels, veins rather than lymphatics. In a specimen killed by pithing, the cephalic lymph sinus was exposed while the heart was still beating; the veins were gorged with blood but the lymph sinus appeared perfectly clear and transparent, and at no time was blood found in the lateral vessels. In several instances a clear fluid was seen to run out of the lateral vessel, when cut, in a fresh specimen.

The arrangement of the lymphatic vesels of *Amia calva* has been found to agree, in general, with that of various other fishes, as described by the several authors, but in some respects there is a marked difference. The system consists of the two parts, a peripheral or subcutaneous and an ental or visceral portion.

To satisfactorily demonstrate these vessels they may be injected but the precaution must be taken to first inject the veins, otherwise the two sets of vessels can not be distinguished with certainty. A convenient place for injecting the

veins is in the large caudal vein which extends along the ventral side of the axon. The tail may be cut off a little cephalad of the base of the caudal fin and the canula easily inserted into the vessel. But as the caudal vein sends off branches into the kidneys, which either break up completely or partially in this organ, the further precaution must be taken to use for injecting some mass that will pass through these small vessels into the cardinal veins beyond. Such a mass may be made by taking 10 grams of gelatin and adding 50 c. c. of water; this is melted over a water-bath and 150 c. c. of water colored with Berlin-blue, is added. This mass becomes fluid at such a low temperature that there is little danger of the gelatinization of the connective tissue of the blood-vessels and their consequent rupture, when injected, as would be liable to occur if the injecting mass melted only at a comparatively high temperature. For injecting the lymphatics, the following mass serves very well. Gelatin, 20 grams; water, 200 c. c.; potassium dichromate, sat. aq. sol. 75 c. c.; acetate of lead, sat. aq. sol. 75 c. c. The gelatin is melted over a water-bath; the hot dichromate is then added after which the hot acetate of lead is added and the whole mass filtered through flannel or absorbent cotton.

LATERAL LINE, LATERAL OR MUCOUS CANAL AND LATERAL LYMPHATIC VESSEL.

In order to avoid any possibility of misapprehension in regard to these three terms it has been thought well to briefly describe them. The lateral line is a longitudinal line along each side of many fishes, marked by the structure or color of the skin, or both. It consists of a row of tubes or pores, mostly on scales, extending from the head to or toward the tail. The pores are the ducts of muciferous glands whose product is excreted on the sides of the fish. (Cent. Dict).

Lateral or Mucous Canal.—In most, if not all, fishes the integument of the body and of the head contains a series of sacs, or canals, usually disposed symmetrically on each side of the middle line, and filled with a clear gelatinous substance. . . . These sensory organs are known as the "organs of the lateral

line," or mucous canals. (Huxley, Anat. Vert. p. 79). The lateral lymph vessel is essentially different from the lateral canal, which has the same direction. If one raises the scales with the lateral canal situated under them, and if the skin be cut, there is found in the subcutaneous connective tissue a small vessel, with delicate walls, lying in the groove which separates the long lateral muscles of the vertebral column and so closely connected to the surrounding parts that it is impossible to separate them. (Hyrtl, Annales des Sci. Nat. Vol. 20 (2e série), p. 222). This canal is the lateral lymph vessel. Unlike the preceding it has no openings upon the surface of the skin.

The main subcutaneous lymphatic vessels of *Amia calva* are four in number and are situated, one on each side of the body, entad of the lateral line, one on the ventri-meson and one on the dorsi-meson. From the large lateral lymph vessels many small branches are given off in a penniform manner. At the base of each pectoral fin is a large lymph sinus. The branches joining these to the lateral lymph vessel extend dorsad and join the latter at the caudal edge of the shoulder-girdle; another branch extends from the pectoral to the pericardial sinus. After receiving the branch from the pectoral sinus, the lateral lymphatic passes under the pectoral arch and opens into a large lymph sinus (Fig. 10), extending from the dorsal end of the clavicle* along the dorso-lateral portion of the cephalic edge of the arch, to which it is closely joined, and into the base of the cranium. In the cranium the sinus could be traced readily only to about opposite the base of the orbit. The opening from this sinus into the veins is at a point about 1 c. m. cephalad, and a very little ventrad, of the dorsal end of the clavicle (Fig. 10). The orifice is guarded by a valve which opens toward the vein. Near the edge of the clavicle, a little ventrad of the level of the lateral lymph vessel, is another orifice opening from this sinus into the peri-

* The clavicle is the large curved bone with a thick cephalic and thin caudal border. It extends ventrad and then cephalo-mesad so as nearly to meet its fellow of the opposite side at the ventri-meson of the throat. (Parker's Zootomy, p. 100).

cardial sinus (Fig. 10). The action of the valve at this opening, as determined by insufflation, permits only the ingress of fluids and it is by this opening, doubtless, that the lymph of the pericardial sinus enters the lymph sinus of the lateral lymphatic vessel, and from thence enters the veins.

At the caudal end of the body the lateral lymphatics terminate in the caudal vein. The correlation of the lymph and blood vessels at this point is somewhat complex. The lateral lymphatic extends caudad, nearly or quite as far as the dorsal fin, when it suddenly bends at right angles and extends between the muscles directly towards the meson. Close to the sides of the vertebrae the vessel opens into a lymph sinus extending along the side of the axon (Fig. 11, s). Consequent on the dorsal inclination of the terminal portion of the axon, the lymph sinus lies at an angle to the general direction of the lateral lymph vessel. In a specimen measuring 53 c. m., the sinus was about 1 c. m., long and from 3 to 5 millimeters at its greatest width. At its cephalic end the sinus opens into the caudal vein. The orifice between the two vessels is closed by a valve which readily permits the flow of lymph into the veins but prevents any flow in the opposite direction as was repeatedly demonstrated by alternate insufflation and aspiration of the caudal vein. The sinus communicates with its fellow of the opposite side by at least two small connecting branches, passing directly from the mesal side of one sinus into the corresponding side of the other. Joining the lateral lymph vessel shortly after it turns toward the meson, is a large branch which extends dorso-caudad to near the dorsal edge of the caudal fin and then turns cephalad and is continued along the body as the dorsal lymphatic (Fig. 11, r.).

The correlation of the lateral lymph and blood vessels was found to be the same on either side of the body.

The lymphatic vessel on the ventral side of the body begins as a large vessel along the base of the caudal fin, and extends directly cephalad till it reaches the level of the heart where it divides into two branches which lie between the pericardium and the tough fibrous partition separating the pericardial from the abdominal cavity. On its course, it receives the

lymph from the anal and pelvic fins. The sinus at the base of each of these fins is smaller than the one at the base of the pectoral. As the vessel approaches the heart it increases in size measuring, in a large specimen, about a centimeter in diameter at the point of bifurcation. The two branches into which it divides merge into the large pericardial sinus which, as already stated, communicates with the sinuses of the lateral lymph vessels and thence with the veins. Possibly there are other openings from the pericardial sinus into the veins but none were observed. In one instance an anastomosing branch was found extending from the large vessel at the base of the caudal fin, to the lateral lymphatic, joining the latter just as it turns toward the meson (Fig. 11, t).

The dorsal lymphatic vessel extends along the dorsimeson from the caudal end of the body to the base of the cranium. At the caudal end, as already indicated, it anastomoses with the lateral lymph vessel, joining it just after the latter turns at right angles to its longitudinal course, to enter the caudal sinus. Whether the dorsal vessel bifurcates into symmetrical branches at its caudal end, can not be positively stated. It is believed, however, that it does. In one specimen a branch was found on either side. At the cephalic end the vessel bifurcates at the base of the cranium, each branch extending laterad to join the large lymph sinus, on either side, which has already been described as extending to near the base of the orbits and into which the lateral lymphatics open. Along the base of the dorsal fin the vessel is somewhat larger than it is farther cephalad. From the relative size of the two extremities of this lymphatic, one might judge that the course of the lymph was caudad, *i. e.*, that this vessel emptied at its caudal rather than at its cephalic end. The fins are well supplied with lymphatics. According to Trois (22), there are two quite large vessels at the sides of each fin-ray. The vessels of adjoining rays are connected by innumerable small anastomosing branches.

THE VISCERAL LYMPHATICS.

The anastomosis of the visceral with the subcutaneous lymphatic system appears to be slight. Only a few of the

smaller branches of the former were filled, however well the latter might be injected. Doubtless by long continued injection of the subcutaneous vessels all the visceral lymphatics could be filled, but a more expeditious method is to inject, by means of a rather coarse hypodermic needle, into one of the small vessels that extends along the intestine or directly into one of the large lymph spaces. It may be said, however, that nothing was found equal to the flexible blow-pipe as a means of demonstrating the course of the lymphatics and their connections with the various trunks. Indeed it is believed that certain of the valves at the orifices could not have been satisfactorily demonstrated in any other manner.

The lymphatic vessels which collect the lymph from the abdominal viscera and convey it to the veins, may, for convenience of description, be divided into two portions of which one consists of three large sinuses and the other of the numerous small vessels emptying into them. Two of the sinuses are situated on either side of the œsophagus immediately caudad of the septum between the abdominal and pericardial cavities; the other extends along the walls of the air-bladder, on the right side.

The sinuses along the œsophagus are separated from each other and also covered on their ventral side by the liver and the pyloric end of the stomach. The left lobe of the liver is joined to the sinus by a broad fold of peritoneum which is attached to the latter along its middle portion. Of the two sinuses the left one is much the larger. In a specimen measuring 53 c. m. in length, it was nearly 8 c. m. long and at least 2 c. m. wide. Its general form is cylindrical. It extends as far caudad as the liver. In general, its attachment to the enteron is along the dorso-lateral portion of the œsophagus and stomach, but it does not extend as far caudad as the latter; it is also closely joined to the adjacent walls of the air-bladder. From the caudal end of the sinus several lymphatic vessels ramify in a rich net-work over the adjacent walls of the stomach and air-bladder. The lymphatic sinus on the right of the œsophagus has the same general form as the one on the opposite side. It is about 5 c. m. in length and 1½ c. m.

in diameter at its widest point. It extends nearly as far caudad as the cholecyst. The cephalic half is covered by the left lobe of the liver; the other half by the cholecyst, to which it is closely united. Several ducts open into the caudal end of the sinus. One duct passes obliquely across the dorsal side of the duodenum and pyloric end of the stomach, and joins the left lymphatic sinus at the apex of the interval between the œsophageal and pyloric portions of the stomach, *i. e.*, near the caudal end of the sinus. This is the only communication that was found between the two sinuses. Another lymph duct, much larger than the preceding, passes ventro-caudad between the pyloric portion of the stomach and the duodenum. Upon reaching the ventral side of the latter it extends directly caudad as far as the spleen where it divides into several small branches which accompany the blood-vessels along the sides of the intestines; along some of the folds of the intestine as many as three lymphatic vessels were found. As the duct reaches the ventral side of the duodenum, it gives off a small branch to the ventral wall of the stomach; the diameter of the main duct itself, along its cephalic portion, is fully ½ c. m.

The last to be mentioned of the three abdominal sinuses, is situated on the right side, along the walls of the air-bladder and stomach. It is fusiform, measuring in a specimen 42 c. m. in length, a little over 7 c. m. from end to end and about 1 c. m. in diameter at its widest point. It opens into the right lymph sinus, on the dorso-lateral side, near the base of the cornu of the air-bladder. There appears to be no valve at this orifice; the injecting material, as well as air, readily passed from the one sinus into the other. At its caudal end it anastomosis with one of the ducts extending along the duodenum; many small branches enter it from the stomach and air-bladder. The lymph from the right and left lobes of the liver enters the corresponding sinus. In only one or two instances were trabeculæ seen in the lumen of these sinuses. Some of the vessels of the intestines anastomose with the peripheral lymphatic system at the caudal end of the abdomen.

As stated before, the large fusiform sinus lying along the

side of the air-bladder, opens into the large lymph sinus at the right side of the œsophagus. The termination of the entire visceral lymphatic system is in the great veins, or ducts of Cuvier, on either side of the heart.

From each of the great lymph sinuses, along the œsophagus, there extend little bay-like prolongations which open into the venous trunks, as just mentioned. In one specimen three of these openings were seen on each side; possibly there were still other smaller ones. The mechanism of the valve-like structures which close these orifices needs further study. The lymph sinuses were repeatedly filled with air, yet but little, sometimes none, was seen to escape into the veins; liquids seemed to pass somewhat more readily. It was found practically impossible to pass a beaded bristle from the lymph sinus into the veins, or the opposite, although the orifice is much larger than the bristle. When the sinuses are distended with air, the thin walls around the openings form slight, rounded swellings, which project into the lumen of the blood-vessel. Immediately around the orifice the walls are somewhat thickened, and as nearly as could be made out these thickened portions over-lap each other, in somewhat the same way as would result if a slit were made in a hollow sphere and one edge drawn over the other. This overlapping of the edges of the orifice would account for the difficulty of passing a bristle through the opening.

THE ENTERIC EPITHELIUM.

The enteric epithelium of this most teleosteoid (in appearance) of Ganoids, as it has been called, exhibits certain morphological features peculiar, so far as at present known, to the group Ganoidei. The buccal cavity is covered by a stratified epithelium; the superficial layers are flattened while the deeper lying cells are more nearly columnar; the intermediate cells gradually merge from the one into the other as is common with this kind of epithelium. At irregular intervals the epithelium is pierced by large conical or dome-shaped structures which project to the free surface. These doubtless correspond to those structures which according to Wiedersheim

"function from the amphibia onwards as organs of taste, while in fishes they probably serve as tactile organs." (Weidersheim, Comp. Anat. of Vertebrates, p. 167). Farther caudad the surface layer of cells gradually becomes columnar with many interspersed beaker-cells. Some distance cephalad of the pneumatic duct-opening the stratified is replaced by a columnar epithelium. The transition between the two is quite sudden there being scarcely any overlaping of the two epitheliums. From this point to within about 2 c. m. of the pylorus, the epithelium is ciliated. Incidentally, it may be mentioned here that ciliated epitheliums have been found in several other regions of the body. In the air-bladder, ciliated cells were found from one end of the organ to the other. The cells are columnar but the cilia are somewhat longer than in the œsophagus or stomach. The ciliary currents extend cephalad or toward the opening of the pneumatic duct. The epithelium of the nasal cavity is also ciliated ; the cells are of the same general form as those of the air-bladder and stomach but the cilia are much longer than in either of the last mentioned organs. It is stated in the Cyclopædia of Anat. and Physiol. (Vol. I, p. 633), that according to Purkinje, Valentin and Steinbuch, the presence of bile arrests the motion of cilia. This is incorrect, in the present instance at least, for cilia were found moving vigorously immediately after emptying the cholecyst of its contents. Ciliated cells were found throughout the whole length of the vesicle and its long convoluted duct. The cilia are quite long and easily seen in both fresh and hardened specimens. The currents induced by the cilia extend toward the opening of the duct.

To form some idea of the rapidity with which foreign bodies are carried along by cilia, a clot of blood was placed on the œsophagus at the level of the pneumatic duct opening ; at the end of five minutes the clot had been carried caudad a distance of 4½ c. m. Farther caudad, the clot moved much more slowly. At the caudal end of the œsophagus is a short region occupied by rather short, broad follicles lined by columnar ciliated cells ; the true gland cells are first met with some distance caudad of the pneumatic duct opening.

According to Schultze (20), the epithelial cells of the stomach in all vertebrates, are open, *i. e.*, the free ends of the cells are not covered by a cell-wall. He thinks that the mucus which these cells secrete is for the purpose of protecting the cells themselves from the digestive action of the secreted fluids. Brinton (3), also seems to hold the same view. He says, "The protection of the stomach from its own secretion is effected mainly by the salivary and other secretions which enter it from the œsophagus and the duodenum. . . . For units of mucous membrane, Fishes seem to have the most powerful gastric digestion." These statements appear somewhat unsatisfactory from the fact that in the American Ganoids, at least, the ciliated character of the epithelium would tend strongly to preclude the formation of a distinct mucous coat over the surface of the stomach. But apart from this, it is believed that the vital properties of the cells are sufficiently potent to withstand any deleterious effects which the gastric secretions may possibly have upon them. Edinger (6), thinks that the functions of the mucus are to thin the chyme and to form a protective covering over the hard indigestible bodies, as sand, shells, etc., which find their way into the stomach. He says that such foreign bodies, surrounded by a tough mass of mucous, are frequently found in the intestine. Ebstein (5), found open as well as closed cells and is of the opinion that during digestion the membrane of the closed cells is ruptured. In all the specimens examined by the writer, both open and closed cells were found.

The surface epithelial cells of Amia's stomach are very slender and the attached ends are continued into long thread-like processes which intertwine with the subjacent mucosa. As already stated, ciliated cells were found uninterruptedly from the œsophagus to within about 2 c. m., of the pylorus; scattered among these were many open beaker-cells. From the open end of many of the latter a mucous mass of varying size was often seen projecting some distance beyond the free ends of the cells. At the cardiac end of the stomach, the gastric glands appear as short tubes, at the base of the follicles mentioned above; they, however, rapidly increase in length,

and over the middle portion of the stomach constitute the greater part of the tubule. As the pyloric region is approached the glandular part decreases in length and disappears about 2 c. m, from the pylorus; from this point to the pyloric valve the glands are lined with cells like those forming the surface epithelium of this region, only shorter. In the cardiac region the mouths of the glands are short and are lined by ciliated cells (Fig. 4).

The cells of the body of the gland are, for the most part, cubical in longisection of the gland, but for a short distance below the mouth the cells are more nearly cylindrical in outline. Several glands may open into a single mouth. In fig. 4 it will be noticed that the cells lining the mouth of the gland are placed obliquely to its long axis. Frequently cells were seen so bent that the angle formed equaled at least a right angle. In all cases the convexity of the cells projected towards the exit of the gland; the attached ends of the cells reached a much lower level than the opposite ends. In the pyloric region the glands are more widely separated from each other; the lining cells of these are situated at nearly right angles to the long axis of the gland. Towards the pyloric valve the glands become shorter and finally disappear near the free edge of the valve. Cilia were not found in the pyloric glands. Near the free edge of the valve-like structure between the stomach and intestine, the characteristic cells of the intestine appear (Fig. 9). They are slender and the basal end is continued into a long thread-like process. The striated border of the cells is very distinct. The varying levels at which the large oval nuclei are situated, give to the epithelium, when viewed in section, a stratified appearance (Fig. 7). The most remarkable feature of the intestinal epithelium, of Amia, is the presence of cilia in the rectum (Fig. 7). The epithelial cells of this portion of the intestine are of the same form as in other parts, but somewhat shorter. The beaker-cells are numerous and their theca are short and rounded. Ciliated cells were found only within a small area immediately caudad of the spiral valve. They may be demonstrated much more easily and satisfactorily in a perfectly fresh condition than after hardening.

SUMMARY.

1. The subcutaneous lymphatic vessels terminate in lymphatic sinuses at either end of the body. The lymph sinuses at the base of the cranium empty into the jugular veins. The pericardial lymph sinus opens into the preceding, the orifice between the two sinuses being guarded by a valve; the flow of lymph is from the pericardial into the cephalic lymph sinus. At the caudal end of the body the lymph sinuses empty into the caudal vein. These sinuses are considerably smaller than the cephalic ones.

2. The visceral lymphatic system is more voluminous than the preceding. In addition to the small vessels extending along the intestines, etc., there are three large lymph sinuses situated, one along the right side of the air-bladder, and one on each side of the œsophagus. The termination of the abdominal lymphatics is in the ducts of Cuvier, there being several openings from each of the lymph sinuses, at the sides of the œsophagus, into the great venous trunks.

3. A ciliated epithelium was found over the greater extent of the stomach and in the rectum; over the whole extent of the cholecyst and its duct; the air-bladder and the nasal cavity.

Thanks are due Prof. Gage for suggesting the subject of this paper, and for kindly criticism of the same.

ITHACA, N. Y.
August 8, 1893.

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DESCRIPTION OF PLATES.

PLATE I.

The outline of the figures, except 10 and 11 were drawn by aid of Abbe's camera lucida. Details were put in free-hand. Objectives used were Leitz Nos. 2, 5, 7, and $\frac{1}{12}$ oil immersion. Oculars Nos. 1 and 3. All figures, except 1, 2, 10 and 11 are drawn on the same scale.

FIG. 1. Section of stomach showing the relative thickness of the different coats. a. mucosa. b. Submucosa and muscularis mucosa. c. Circular muscular layer. d. Longitudinal muscular layer.

FIG. 2. Gastric gland.

FIG. 3. Epithelial cells of stomach. a. Ciliated cells. b. Beaker-cells with mass of exuded mucus.

FIG. 4. Mouth of gastric gland showing the ciliated epithelium with which it is lined; also two glands opening into a single mouth. a. Beaker cell.

FIG. 5. Transection of gastric glands.

FIG. 6. Longisection of gastric gland.

PLATE II.

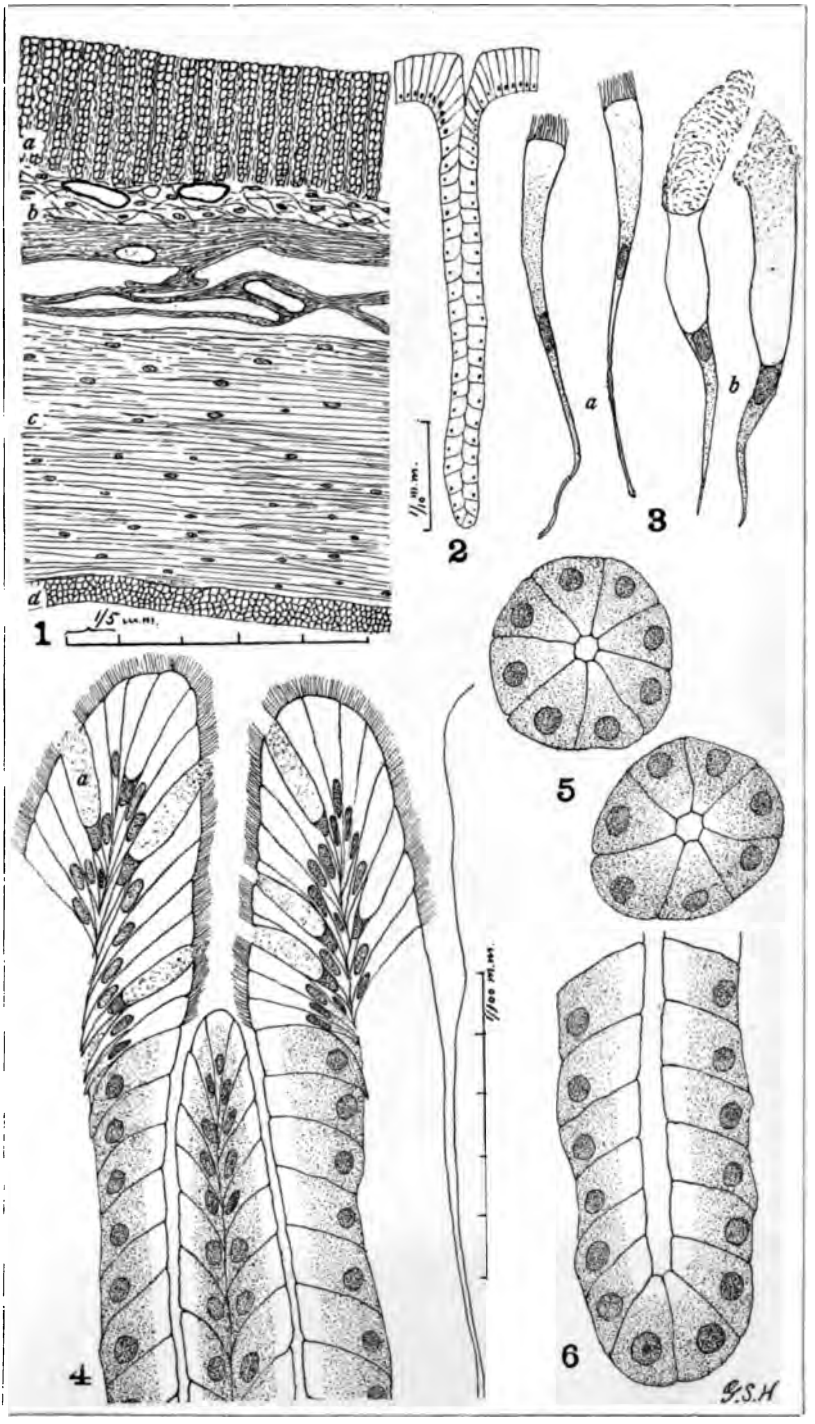
FIG. 7. Ciliated epithelium of the rectum, showing ciliated and beaker-cells and the nuclei at various levels.

FIG. 8. Cells of rectum as seen on end. b. Columnar cells. c. Beaker-cells.

FIG. 9. Epithelial cells of intestine showing form of cells and striated border. d. Beaker-cell.

FIG. 10. Diagram of head of Amia showing the connection of the subcutaneous lymphatic system with the veins; the operculum has been removed. a. Pectoral arch. b. Cephalic lymph sinus. c. Jugular vein. d. Duct of Cuvier. e. Lateral lymphatic. i. gill. p. Pectoral fin. s. Serrula. By looking closely at the diagram of the lymph sinus, the connection with the vein may be seen. Caudad of this is another opening into the pericardial sinus; the pericardial sinus itself is not represented, only the orifice between the two being figured.

FIG. 11. Diagram showing the relation of the subcutaneous lymphatic and venous system at the caudal end of the body. a. Dorsal fin. b. Caudal fin. d. Anal fin. e. Axon. i. Caudal vein (the caudal artery has been omitted). l. Lateral lymphatic vessel; the one on the opposite side is indicated by broken lines. s. Caudal lymph sinus. The opposite one is indicated by dotted line. o. Lymph vessel at base of caudal fin. This is continuous with the lymphatic along the ventri-meson as shown in diagram. t. Connecting branch between the lymphatic vessel at the base of caudal fin and the lateral lymphatic vessel. r. Branch connecting the dorsal and lateral lymphatic vessels. n. Dorsal lymphatic vessel. v. Lymph vessel along ventri-meson.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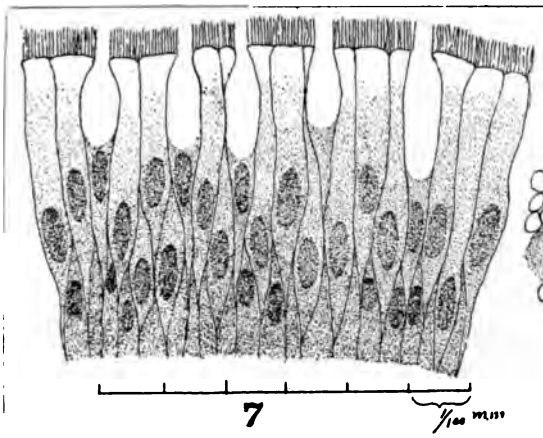

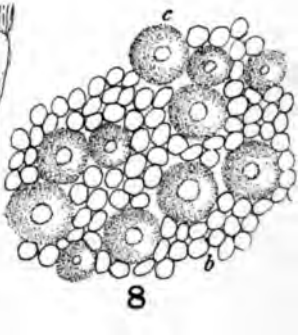

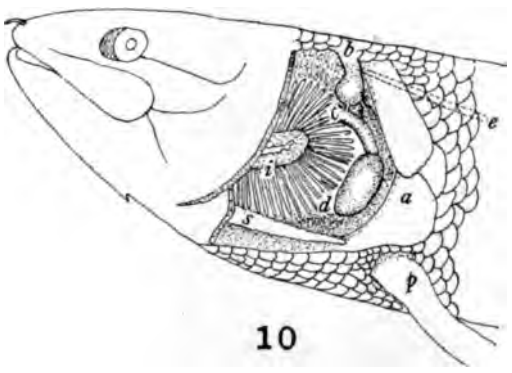

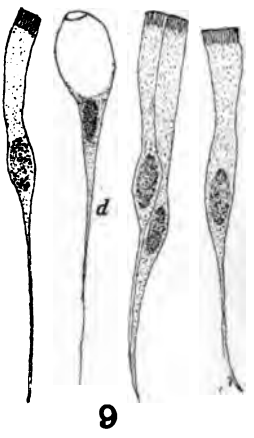

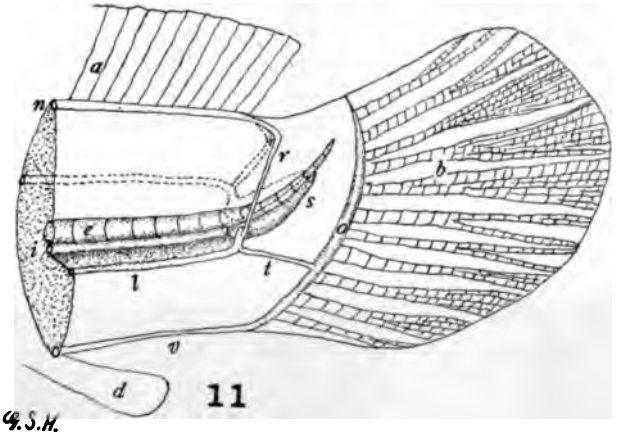

G.S.H.

BRAIN PRESERVATION, WITH A RÉSUMÉ OF SOME OLD AND NEW METHODS.

By PIERRE A. FISH.

The brain, the organ of thought, complex in structure, the great co-ordinator of bodily functions, the master and yet the servant of the animal economy, has been the last of the viscera to receive careful preservation. The ancient Egyptians in their most *perfect* embalments "drew the brain through the nostrils partly with a piece of crooked iron and partly with the infusion of drugs." The other viscera upon removal were carefully cleansed and after proper treatment were replaced in the body, the brain apparently being the only part rejected.

The summary treatment of this important organ and the bad precedent thus established by the Egyptians retarded for a long time the development of any progressive ideas in this direction. From the time of the Egyptians down to near the close of the seventeenth century no advance but actual retrogression occurred in the art of preservation; this being due to some extent to the indifference of the nations in power at that time, but chiefly to the great religious opposition toward anything pertaining to science. During this dark period of scientific stagnation much has been lost that may never be recovered.

The crude and erroneous descriptions of the early anatomists justify the belief that their methods were but little superior to those that preceded, but the progress in those early years of embalming the body, marks also an advance, slight and inefficient perhaps, but nevertheless an advance, in the preservation of the brain itself; particularly so when the injection method came into use. To a Hollander, Frederic Ruysch, Professor of Anatomy, at Amsterdam from 1655 to 1717, belongs the honor of having originated and perfected this method to such an extent that his specimens are said to have been wonderfully life-like and to have aroused the admiration of the people of his age. The formula of his preservative was not divulged and the secret of its preparation died with him.

William Hunter did much to extend the practice of injection by producing some very beautiful specimens and the impetus thus given by these early anatomists has brought the method down to us with but few if any radical changes.

Admirable as these results were concerning the body as a whole, it became apparent that they were quite inadequate when a more thorough and accurate knowledge of brain morphology was demanded, thus it came about that greater care was used in the removal of the brain and special methods of treatment were devised, and the importance of technique became more and more emphasized, especially so within the last two or three decades.

The consistence of the brain coupled with the difficulty of its removal renders it a difficult organ to preserve. History gives good evidence that the advance in the knowledge of brain structure has been largely dependent upon improved methods of manipulation.

The purpose of hardening is to bring the brain into a proper condition for the continued study of either its fine or gross anatomy, the former usually requiring some special care in methods and after-treatment which may be dispensed with in the latter without apparent detriment.

For the study of the gross anatomy either wet or dry preparations may be available. The preference generally being given to the wet since they are more easily and quickly prepared and because they admit of further and careful dissection at any time after once being well hardened. A shrinkage in the tissues must necessarily occur during this process but it is not usually carried so far as in the case of the dry preparations. Nor is there such an unnatural color unless some colored preservative is employed. But there is the disadvantage of a possible ruination of the specimens by over-exposure to the air, evaporation or deterioration of the preservative and a consequent expense in renewing the same.

For the study of surface anatomy and of certain parts dissected out before the specimen is "dried," there is no reason why, if successfully prepared, the dry method would not answer most needs and have the further advantage of remaining permanent in the air.

Reil's method of preparing the brain : *

"Of the methods which I have employed in preparing brains those contained in the following directions answer best : (1). Let the brain be hardened in alcohol and then placed in a solution of carbonated or pure alkali, in the latter two days, in the former for a longer period, and then again hardened in alcohol if thus rendered too soft. The advantage of this method is that the fasciculi of nervous matter are more readily separable and the brown matter more distinguishable from the white than after simple maceration in alcohol ; the gray matter is rendered by the alkali of a blacker gray and assumes the consistence of jelly. (2). Let the brain be macerated in alcohol in which pure or carbonated potass. or ammonia, has been previously dissolved ; the contraction of the brain is lessened by this process. (3). Let the brain be macerated in alcohol from six to eight days and then its superficial dissection commenced, and the separation of the deeper parts continued, as the fluid in which the brain is kept immersed, penetrates its substance. This method appears to me better than the preceding, and would very likely be improved if the alcohol were rendered alkaline. The fibers in a brain thus prepared are more tenacious than otherwise, and the deeper parts are sooner exposed to the influence of the alcohol."

These methods are applicable chiefly for the macroscopic study of commissural relations and the general direction of fibers.

J. Müller in 1834 recommended the use of creosote water for the preservation of the brain and myel.

Alcohol is the oldest and most universal preservative employed. It has good "fixing" properties but needs considerable attention in order to produce the best results. For fixing, it is frequently used in conjunction with some of the various salts, or in case some non-alcoholic fixer is used, it supplements or completes the hardening thus begun. As a preservative it is generally used at the ordinary commercial strength —ninety to ninety-five per cent., although for most tissues eighty or even seventy-five per cent. seems to suffice.

On account of the continuous dehydration and the struct-

* Mayo's translation of Reil's Eighth Essay.

ural changes induced thereby, it is advisable to use not higher than ninety per cent. The great and unequal attractive power of alcohol for water, renders it necessary to begin with the lower grades. Otherwise the rapid withdrawal of the water before the alcohol can replace it, will cause shrinkage and the tearing or breaking down of the tissue. Immersion of a large specimen in a limited quantity of strong alcohol is likely to induce a rapid hardening of the surface, forming a crust through which the alcohol may cease to penetrate, causing a consequent maceration of the interior.

For general utility, economy and certainty of result, no reagent excels potassium bichromate in its action on nervous tissue. It is said that attention was called to this salt for hardening purposes by a Mr. Savory, some thirty or more years ago[16]. It is commonly used in a simple two or five per cent. solution or in the form of "Müllers" or "Erlicki's" liquids. The simple solution has of late come into greater prominence.

It is inexpensive; it hardens slowly but thoroughly, with a minimum of distortion and leaves the specimen in a state of good consistency even if its action is prolonged. Its application is general; it preserves the contours of large and irregular areas for the morphologist and maintains the proper relations of the structural elements for the histologist. A little chromic acid (one or two drops of a one per cent. solution) added to each thirty cubic centimeters of the bichromate will do no harm and will quicken the hardening.[13] All chromic salts impart a disagreeable and abnormal color to the specimens and for some purposes render them quite undesirable.

This[16] it is said may be obviated to some extent by hardening the tissue in the following mixture:

Potassium bichromate	6 grams
Potassium nitrate	4 grams
Water	180 c. c.

After-treatment with absolute alcohol is recommended by W. C. Krauss for decolorization. Unna advises peroxide of hydrogen. Lee mentions chloral hydrate in a one per cent.

solution, but this is declared by Gierke to be prejudical to the preservation of the tissues.

Corrosive sublimate is useful as a fixative either in an aqueous or alcoholic solution ; it is more soluble in the latter. Chaussier at the beginning of the nineteenth century recognized the antiseptic properties of this salt and since that time it has been quite extensively used as a preservative. Professor Robert Garner[8] with regard to his method says : " *We* let the brain fall from the skull into a hardening solution of bichloride of mercury, the strength about six ounces of the salt to the half gallon of water making a fluid of about 1.038 sp. gr. or the same as the brain itself, in which it consequently remains suspended in mid-fluid without pressure on any of its surfaces and becoming hard and solid without the contraction which takes place when spirit is used. "

Richardson[16] gives the following formula for the central nervous system :

Mercuric chlorid	2 grams
Alcohol (sp. gr. 83)	90 c. c.
Hydrochloric acid.	2 c. c.

There are various inconveniences attending the use of this reagent, not the least of which are its corrosive action on anything metallic making it very necessary that all traces of it be washed out before any dissection is undertaken ; its caustic action on the hands is very marked ; precipitates often occur in the tissue and are a source of considerable annoyance to the histologist. Camphor renders the sublimate more soluble and if the tissue after its sublimate bath be brought into alcohol containing camphor the washing out of the salt is considerably expedited. Tincture of iodine is another agent useful in this respect. A little of it is added to the alcohol and as it dissolves out the sublimate, the color of the solution is weakened and the iodine is gradually renewed until the color no longer fades. The alcohol should be changed frequently. If the sublimate is not thoroughly removed from the tissues they become brittle.

The origin of the use of Zinc chlorid for neurological purposes is enveloped in considerable uncertainty. Bischoff* in a

*Die Grosshirnwindungen des Menschen. München. 1868. S. 11.

note says: "From a note in Gratiolet (Mémoire sur le plis cérébraux de l'homme. Paris. 1854, p. 11.) it is to be seen that a Parisian modeller, Stahl, likewise used the zinc chlorid for hardening brains, in order to make a cast of the same afterward, but it does not appear that Gratiolet employed the same process in his anatomical researches." Bischoff himself had used it for some years previous to 1868.

It is a deliquescent salt and specimens should not be left too long in its solution lest they soften. The hardening is continued in alcohol. Aqueous solutions are generally used since enough of the salt may be dissolved to support the brain. Broca[3] (1879), was perhaps the first to recommend it in an alcoholic solution (ten per cent.). It acts here as a very strong dehydrant, but its action is even if rapid, and with careful treatment no marked distortion results. It has also proven eminently satisfactory for histological work, but for this a five per cent. solution is apparently just as efficacious as the stronger. The specific gravity of a saturated alcoholic solution is not great enough to buoy the brain, and a bed of cotton is therefore necessary.

Glycerin makes a very efficient preservative. It is, however, generally utilized as an adjunct in methods more or less complex or for the immersion of specimens that have already been hardened.

Nitric acid in a ten or twelve per cent. solution has also been recommended; the specimen is to be immersed from twelve to fifteen days and turned frequently as the liquid is too dense to admit of its being entirely covered. This reagent is said to give the *toughest* of preparations.

Experiments were made in May, 1892, to determine approximately the relative loss of weight and girth of a number of sheep brains prepared in different ways. The girth was ascertained by measuring transversely around the brain at the level of the temporal lobes. This as well as the weight was determined at three stages during the course of hardening: first, when fresh; second, the intermediate stage, or before the specimen was brought into alcohol; third, after immersion in alcohol for a longer or shorter time. The accompanying table shows very concisely the results thus obtained.

Fluid.	Weight.			Girth.		
	Fresh.	*Intermediate.*	*Alcohol.*	*Fresh.*	*Intermediate.*	*Alcohol.*
1. Zinc chlorid, ... 200 grams, 70 per cent. Alcohol . 3000 c. c., Glycerin, ... 1200 c. c., Sp. gr. 1.05.	114 grams May 2, '92.	87 grams May 9, '92.	78 grams May 12.	16.4 cm.	15.2 cm.	14.5 cm.
2. 10 per cent. aqueous solution of Zinc chlorid, Sp. gr. 1.14,.	112 grams May 2.	93 grams May 24.	67 grams June 11.	16.8 cm.	15. cm.	14.5 cm.
3. Equal parts of a saturated aqueous sol. of Potassium bichromate and a 10 pr ct. aqueous sol. of Zinc chlorid.	110 grams May 2.	96 grams May 9.	71 grams June 11.	16.5 cm.	15.7 cm.	15.2 cm.
4. Saturated aqueous solution of Corrosive sublimate, Sp. gr. 1.05, . .	112 grams May 2.	118 grams May 24.	76 grams June 11.	16.9 cm.	16.9 cm.	14.9 cm.
5. Equal parts of saturated solutions of Potassium bichromate and Corrosive sublimate, (aqueous) . . .	100 grams May 2.	108 grams May 9.	75 grams June 11.	15.9 cm.	16.5 cm.	15.3 cm.
6. Saturated aqueous solution of Potassium bichromate, Sp. gr. 1.06,	101 grams May 2.	115 grams June 11.	94 grams Sept. 19.	15.9 cm.	16.6 cm.	16. cm.

The brain "fixed" in fluid No. 1 did not sink to the bottom of the vessel until after six days. Within ten days it had lost 36 grams in weight, and 1.9 centimeters in girth, and had become slightly distorted. The specimen in fluid No. 2 floated for more than a week; it also became somewhat distorted. The loss of weight was 45 grams, of girth 2.3 centimeters, being greater than in any of the others. Fluid No. 3 was very rapid in its action and produced a very firm preparation. The color was considerably lighter than in the ordinary bichromate specimens. The loss of weight was 39 grams, of of girth 1.3 centimeters. It should be noted with regard to fluid No. 4, that the weight increased 6 grams at the intermediate stage and that the girth was exactly the same as when fresh. At the third stage, however, there was a loss of 36 grams in weight, and of 2 centimeters in girth, due without doubt to the re-dissolving of the sublimate in the alcohol. Fluid No. 5 gave a better final test than did any of the preceding. There was an increase of 8 grams in weight and of 0.6 centimeter in girth at the intermediate stage. The loss of weight was 25 grams and of girth 0.6 centimeter. Treatment with fluid No. 6 left the brain nearest to its original weight and girth. There was a gain of 14 grams in weight and of 0.7 centimeter in girth at the intermediate stage. After more than four months from the date of its first treatment it had lost only 7 grams in weight and had *gained* 0.1 centimeter in girth. The bichromate is nearly insoluble in alcohol, and once having penetrated the tissue thoroughly, it remains; the replacement of the natural water of the tissues is so gradual that there is little or no chance for shrinkage, while the alcohol afterward helps to keep the salt in place if kept in the dark (Virchow). The alba and cinerea are quite markedly differentiated; and there always exists the abnormal but characteristic chromic color.

An ideal preservative would be one of about the same specific gravity as the brain itself, replacing gradually the natural fluids of the tissue with a simple fluid, or with a solution of some salt of equal density, and not markedly changing the natural color or size of the specimen.

There are two liquids which will cause the brain to retain approximately its normal size; one is glycerin which, after it has thoroughly infiltrated the hardened tissues, causes them to absorb moisture from the atmosphere and the natural fluid is thus artificially replaced by means of this hygroscopic agent. There must, however, be some limit to the preservative action, and the time may eventually come when enough water will have been absorbed to cause considerable deterioration. The other liquid is potassium bichromate which, as noted in the table, caused an actual "bloating" of the tissue, increasing both the weight and girth of the specimen, and imparting an undesirable as well as an unnatural color. The pia is a more or less inelastic and pervious membrane, and while on the one hand it may retard the penetration of the fluid, it serves a little later, in the case of the bichromate to restrain the "bloating" and keep the tissue within bounds. The pressure either from without or within, would tend to disturb the normal relations of the histological elements.

Brains from animals of the same species react differently although subjected to exactly the same course of treatment. The density of the tissue, the age and condition of the subject, the temperature and many other factors equally important, are causes which contribute to these varying results.

After considerable study and experimenting a fluid was devised, which, though not ideal in its effects, seems to answer the requirements of economy, fixation of the structural elements, differentiation of tissue, a minimum amount of distortion, firmness of texture, and rapidity of action.

The formula is as follows:

Water	400 c. c.
95% Alcohol	400 c. c.
Glycerin	250 c. c.
Zinc chlorid	20 grams.
Sodium chlorid	20 grams.

The specfic gravity of the mixture should be about 1.04, a little greater than that of the brain itself (1.038). The

slightly greater density of the fluid is believed to be more advantageous than otherwise, since it buoys the brain until the tissue has begun to harden and can partially support its own weight. The pressure is nearly enough equal on all sides to prevent any noticeable change of form. It is recommended that the cavities of the brain be filled with the mixture (cœlinjected) and if practicable the blood-vessels also injected. After an immersion of about three days the specimen should be transferred to equal parts of the foregoing mixture and seventy per cent. alcohol for a week or more, where on account of the lesser specific gravity it should rest upon a bed of absorbent cotton; it is finally stored in 90% alcohol.

The addition of the zinc chlorid to the solution is to expedite the hardening, to differentiate the tissue, and to insure a more equable and penetrating action. Osler attributes the differential effect to the glycerin or some impurity in it. Experiment has not confirmed his statement. Zinc chlorid coagulates the blood and renders it much darker than usual. The highly vascular condition of the cinerea would soon render it susceptible to the action of this salt, and it would in general assume a shade relatively much darker than the alba. The sodium chlorid is supposed to render the zinc more soluble, and to some extent to lessen its causticity. The glycerin is also useful in this latter respect, but its chief use besides preservation is to bring the fluid up to the required specific gravity.

A one-fifth per cent. solution of picric acid in fifty per cent. alcohol has been used by Professor S. H. Gage with very successful results upon a human brain. The specimen was carried up gradually to 95% through the intermediate grades of alcohol. He has also obtained excellent preparations of fetal brains by injecting the preservative through a hypodermic needle into the brain cavities.

"Dry" preparations are those which may remain permanently exposed to the atmosphere at the ordinary temperature, without apparent detriment. There are essentially two methods of preparation, the one consisting of actual dessication or mummification, in which the specimens remain hard and

inflexible ; the other involves the infiltration of the tissue by some hygroscopic substance like glycerin which replaces the natural fluid by abstracting the requisite amount of moisture from the air. Such specimens, of course, are not dehydrated and therefore are not *dry* in the same sense as those of the former class.

A temporary dry preparation of the brain for demonstrative purposes has been recommended by von Lenhossek[21]. After thorough hardening in alcohol, the specimen, when needed for demonstration, is carefully dried in soft linen and then coated with a thin layer of celloidin applied with a fine brush. After five or ten minutes the celloidin dries, and as a thin, transparent, tough membrane affords great protection and firmness to the preparation. If exposed to the air for more than two hours the specimen will begin to shrink and should be returned to the alcohol.

Paraffin impregnation of brain tissue for dry preparations was first employed by Fredericq[7]. Schwalbe[18] in the same year (1876) adopted Fredericq's method slightly modified. The brain is hardened in zinc chlorid or alcohol, the membranes are removed and the specimen cut into suitable pieces, impregnation *in toto* does not seem to be advisable. After dehydrating in strong alcohol, immerse in turpentine until completely saturated, then infiltrate with soft paraffin at a temperature of 60° C. from five to eight days and let cool on a layer of cotton taking care to avoid deformation. W. C. Krauss[11] and others have employed a similar method and recommend it for friable specimens.

Dr. J. W. Blackburn's[1] method consists of allowing the specimen to harden for about five weeks in Müller's fluid, the pia being removed after a few days immersion. After thorough dehydration in alcohol it is placed in a saturated solution of Japan wax (a concrete oil, the product of *Rhus succedenea*) in chloroform. When the alcohol has been displaced the specimen is transferred to a bath of pure melted wax and kept there at the melting point (42° to 55° C.), until thoroughly infiltrated. Upon removal the wax drains from the surface leaving it perfectly smooth. A small proportion of paraffin will prevent cracking.

Stieda[19] immerses the brain in an aqueous solution of zinc chlorid for twenty-four hours, as soon as it becomes firm enough the pia is removed and the specimen is transferred to ninety-six per cent. alcohol for two or three weeks, to dehydrate, it is then transferred for an equal length of time to turpentine and finally immersed for two weeks or longer in the ordinary commercial oil-finish. It is laid on blotting paper to dry for about eight days, and acquires a dull brown color on its surface. A shrinkage occurs which he considers unimportant, about one fourth of the original volume being lost.

Teichman[19] has pursued a similar course, the difference being that the brains were hardened in alcohol and finally impregnated with "Damar-harz" or "Damar-lack."

So far as Stieda knows Broca was the first to use nitric acid for hardening the central nervous system. His formula is as follows:

Water.....5 parts.
Nitric acid.....1 part.

The brain is left in this mixture for two days; the quantity of the nitric acid is then doubled and after two days more the specimen is taken out and allowed to dry and harden. There is considerable shrinkage. A method of "galvanoplastie" devised by M. Oré[3] is said to give good and durable specimens. Duval has proposed a modification of Broca's method in that the specimen is finally to be infiltrated with paraffin.

Hyrtl[10] (1860) saw no special advantage in using salts or nitric acid combinations, and gave the preference to alcohol; the addition of sugar as recommended by Lobstein gives to the specimen a welcome degree of flexibility. His experiments on dry preparations were not wholly satisfactory; the brains of a horse and calf were utilized and after hardening in sublimate were "cooked" in linseed oil and then allowed to dry. They kept their shape for a couple of weeks but after some months the horse brain shrunk to the size of a small apple and that of the calf to the size of a nut.

Giacomini[9] was the first to use glycerin for "dry" preparations; his specimens have been highly commended for retain-

ing their volume and color to a remarkable degree. All glycerin methods are essentially the same in principle and differ from Giacomini's chiefly in the manner of hardening and manipulation. Giacomini prefers a saturated aqueous solution of zinc chlorid for hardening although potassium bichromate, nitric acid or alcohol will give good results. The pia is removed after an immersion of twenty-four hours in the zinc chlorid solution, the brain remains in the liquid for two or three days longer, until it tends toward the bottom of the vessel, when it should be removed, as a longer stay would cause it to absorb too much water, it is then transferred to 95 per cent. alcohol where it may remain indefinitely, ten or twelve days usually being sufficient. The specimen is finally put into pure glycerin or glycerin containing carbolic acid to the amount of one per cent., when it has sunk just below the surface it may be removed and exposed to the air. After a few days when the surface has become dry, it is varnished with india rubber or better yet with marine glue varnish diluted with a little alcohol. This completes the process.

Dissections should be made previous to the glycerin bath. Histological detail is also said to be preserved to a remarkable extent.

Laskowsky's[12] method consists of first washing the fresh specimen in water to remove the blood, it is then placed in the following mixture :

Water	100 parts.
95 % Alcohol	20 parts.
Boracic acid	5 parts.

Kept in a cool place.

The pia is removed and the brain then placed in a saturated alcoholic solution of zinc chlorid for five or six days, the bottom of the vessel being covered with cotton.

Transfer for fifteen or twenty days to a mixture consisting of :

Glycerin	100 parts.
Alcohol	20 parts.
Carbolic acid	5 parts.
Boracic acid	5 parts.

Let the specimen dry in the air, protected from dust.

Max Flesch[6] recommends the addition of one part of corrosive sublimate to three thousand parts of glycerin. A human brain he leaves in water for two days in order to wash out the blood, it is then placed in alcohol for four weeks; then for two weeks in equal parts of glycerin and alcohol and finally four weeks in pure glycerin, to every three thousand parts of which is added one part of corrosive sublimate (the sublimate is dissolved in a small quantity of water and alcohol and then added to the glycerin). Wherever it is necessary the brain is supported upon a layer of cotton to avoid deformity.

After the drainage of the superfluous glycerin the specimen is again placed for final storage upon a piece of blotting paper supported by a layer of cotton and the whole enclosed by a paste board box with a glass top, to protect from the dust. The expense is slight as the solutions can be used repeatedly. The alba and cinerea are said to remain well differentiated.

Struthers[20] hardens the brain in alcohol after the removal of the membranes, for ten or fourteen days. It is then put into :

Glycerin . . . . . 4 parts,
Carbolic Acid . . . . . 1 part.

for two or three days. When the superfluous glycerin drains off, the brain is put under a glass case in order that it may not take the dust. It is claimed that there is less shrinkage and more flexibility than in Giacomini's method.

Richardson[16] recommends the following formula :

Glycerin . . . . . 300 c. c.
Methylated spirit . . . . . 600 c. c.
Zinc chlorid . . . . . 2 grams.

" Dissolve the zinc chlorid in the spirit and gradually add the glycerin. In use immerse the structure in the solution and keep it in until it is fully saturated. Then remove and let harden," [dry].

As a result of numerous experiments and a careful study of previous methods, the following process was devised : The preliminary treatment is as directed on page 393. After dehy-

dration in repeated changes of ninety-five per cent. alcohol, immerse the brain in a mixture of:

Turpentine . . . . . 3 parts,
Castor oil . . . . . 1 part,

until it becomes tolerably translucent (one or two weeks) changing the solution if it becomes cloudy, then transfer to pure castor oil for a week or two. Allow it to drain on a layer of cotton covered with absorbent paper until the surface dries and then paint it over a few times with an alcoholic solution of bleached shellac. The specimen soon becomes firm and requires no special attention when once it has become dry. This process differentiates alba and cinerea well. (See Plate). The brain sections or dissections should be made before immersing in the turpentine-oil mixture. It will be found that the alba becomes translucent first, the preparation at this particular stage may then be put into the pure castor oil until thoroughly penetrated and subsequently drained and shellaced. The castor oil may be used repeatedly and costs only one-half as much as glycerin.

Some shrinkage occurs, the dry specimen losing about one-fourth of its volume after it has left the liquid. It should be remembered that the brain consists of eighty-eight per cent of fluid and that the possibilities of evaporation and the replacement of this natural liquid by an artificial one as in dehydration render some shrinkage inevitable. It is not feasible therefore to harden a brain rapidly without some condensation of tissue, the main point is to harden the specimen without distortion or to have the shrinkage evenly distributed. Theoretically the shrinkage might be lessened or entirely obviated if each fluid or mixture into which the brain is immersed could be kept at the same specific gravity as the brain itself, and replace equally its normal fluid. This does not seem to be practicable where dehydration is necessary. The dry process has given good results on delicate fetal brains, it seems to strengthen them so that they may be readily handled, but great care must be taken in transferring them through the different fluids. If breakage should occur the

parts may be stuck together with mucilage and after shellacing again the specimen will be as durable as ever.

There are objections to both the dry and glycerin methods. The former renders the specimens too hard and there is perhaps a little more shinkage; with the latter there is more flexibility but there is a greasy and disagreeable feel to the preparations. Experiments are in progress with a view toward combining the more desirable features of each, by compounding an emulsion in the following proportions:

Glycerin	100 c. c.
Castor oil	100 c. c.
Gum arabic	50 grams
or,	
Gum tragacanth	50 grams

If well made it does not "crack" and seems to penetrate the tissues quite well though somewhat slowly. The emulsion can be used repeatedly by rubbing it up again in a mortar before putting a new specimen into it. The brain may be shellaced as in the previous method.

The writer wishes to acknowledge his obligations to Professor Wilder whose kindly interest in this line of work has rendered practicable many interesting experiments and whose indefatigable energy in scientific research has been an example as well as an incentive in the preparation of this paper. Acknowledgments are also due to Professor H. H. Donaldson of Chicago University and to Professor S. H. Gage of Cornell for valuable suggestions.

ITHACA, N. Y.
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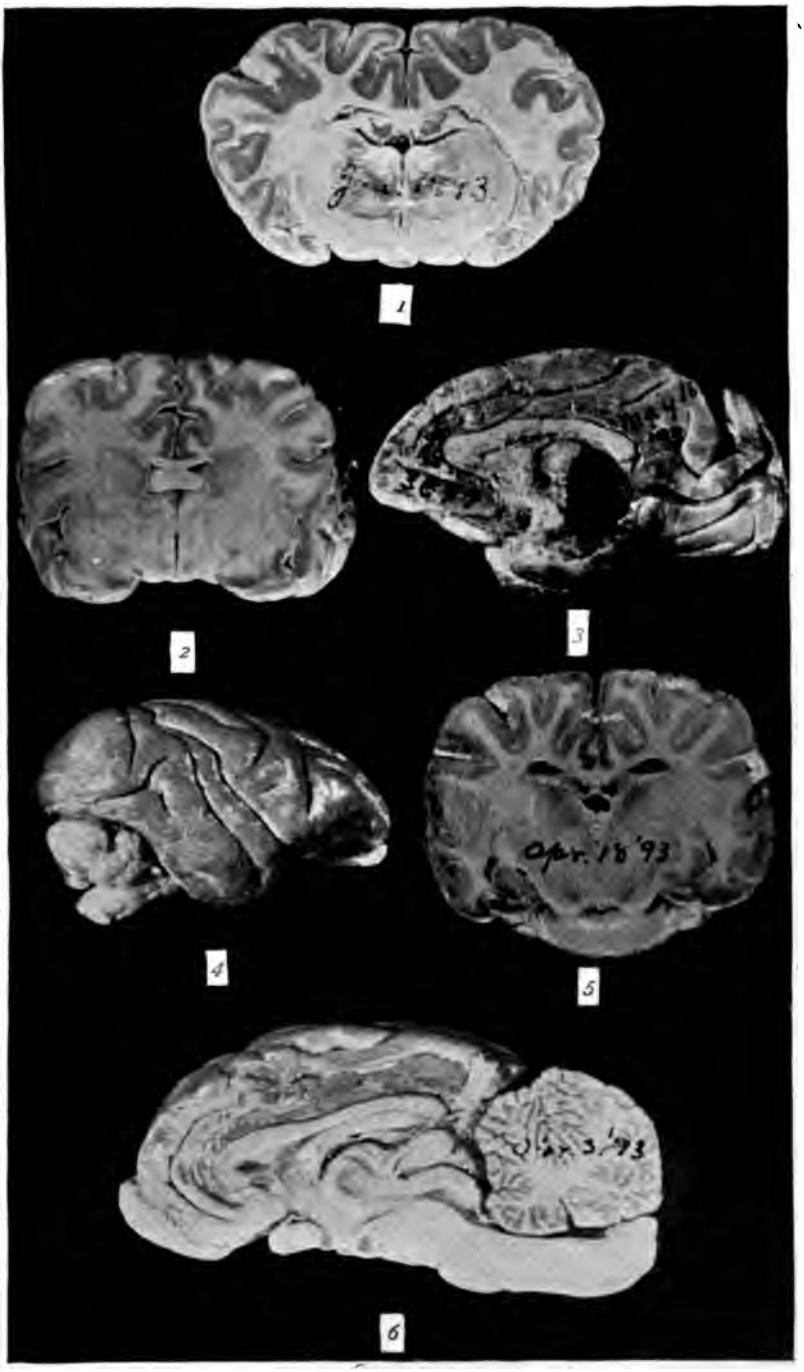
DESCRIPTION OF PLATE.

All of the figures are at about the natural size of the dry specimens and were prepared according to the castor oil method.

The transections show the differentiation of the alba and cinerea.

Fig. 1 and 6 are from the sheep, *Ovis aries*. Fig. 2 and 5 are from the dog, *Canis familiaris*. Fig. 3 is the mesal view of the right hemicerebrum of *Macacus rhesus*. Fig. 4 is the lateral aspect of the right hemicerebrum of *Macacus cynomolgus*.



DRY PREPARATIONS OF THE BRAIN—FISH.

Cretaceous of Europe, indeed prove these forms to be of very ancient origin. Zostera is by far the best known genus and is apparently one of the oldest types. It is the only genus of the group which has species at all cosmopolitan in their distribution. One of these, Zostera marina, frequent in the old world, extends to the shallow bays and tide-water coves of Atlantic North America, and is the only sea-grass found in its waters. The distinguished morphologist, in whose honor this paper was written, will recall the submarine meadows of Zostera along the New England coast as giving shelter to numerous forms of animal life. The wide extension of this species and Zostera nana, an old-world form, so far as definitely known, shows Zostera to be the most flexible and the strongest of the old types believed to exist in the Tertiary seas.

From this strain only one other subsidiary type of generic importance—Phyllospadix, appears to have sprung and persisted till recent times. This genus and Zostera are characterized by a flattened spadix, closely invested by the spathe, in which the flowers are entirely concealed until anthesis. The monœcious spadices and ovoid fruits of Zostera are replaced in Phyllospadix by diœcious spathes and cordate-sagittate fruits. The retinacula, or appendages protecting the sexual organs, wanting in some Zosteras, small in others, are strongly developed in Phyllospadix.

Some years ago, while in Berlin, my attention was particularly called to the genus under consideration, while looking over with Professor Ascherson the drawings for his monograph of the order in the "Pflanzenfamilien." I was then chiefly struck with the fact that the genus was a nearly monotypic one and peculiar in its geographical restriction. When the plants were first seen growing along the bold shores of Santa Cruz county, one was most impressed by the remarkable departure from Zostera in habitat. Like many of the great Algæ, it is either a surf plant living on exposed rocky points, or grows in coves of rocks and sand, where the strong movement of the waters keeps the long, supple leaves constantly doubling upon themselves.

As this paper concerns itself with the morphology, anatomy

and environment of the genus in relation to its probable origin, I will dismiss, for the present, the question of the species with the following remarks: The two species of the California coast have been collected about Monterey Bay, and somewhat carefully examined together with dried material collected along the coast from Oregon to Santa Barbara. They are closely allied forms, although it will be convenient to refer to them as distinct species. Phyllospadix Scouleri, described as early as 1840 by the elder Hooker from Scouler's specimens from the Columbia River, inclines to bolder shores, has a flatter leaf, often but not always a much shorter stem, with one spathe (occasionally several), and usually larger fruits than Ph. Torreyi, Watson. The statement that the leaf is broader does not always hold, and three nerves are present in both, instead of only in Ph. Scouleri, as is usually stated. They are more obscure in Ph. Torreyi on account of the leathery texture of the latter, thrice as thick as in the sister species. The very doubtful Ph. serrulatus, Rup., I have not seen, and nothing seems to be known of it beyond the fragment on which Ruprecht based his description.

What follows concerning the morphology and structure of the genus relates to Ph. Torreyi, reference being made to the second species by especial mention.

Phyllospadix grows attached to rocks, or to a rocky substratum covered with a few inches of sand, in distinct turfs or flat tussocks usually, each being from one-fourth to one-half a meter in diameter, and composed of branched, rooting rhizomas giving rise to the long leaves among which are concealed the much shorter spathe-bearing stems. It is not often seen extending more than one or two fathoms beyond low-tide. At very low water a fringe of plants along the upper margin of the belt is often left completely exposed, but ordinarily the plants are not left quite bare. They cling by means of short, firm roots and the under-surface of the somewhat interwoven rhizomas, to hard surfaces, somewhat after the manner of the larger Algæ; and although the stems and leafy branches break away, the rhizomas seldom loosen their hold except with age.

The rhizoma and the arrangement of its dependent mem-

bers appear never to have been described. Bentham and Hooker, in the Genera Plantarum, describe the rhizoma as tuberous-lobed. Ascherson uses a similar expression, and Morong's recent figure shows a tuberous body at the base of the stem. This error has come from the examination of herbarium specimens, where the rhizomas usually appear broken into knotty masses. There is no suggestion of tuberous or bulbous formations about any living specimen. The growth is monopodial, and one can obtain specimens from ten to twenty-five centimeters in length, the usual thickness being about one centimeter. Referring to Plate I., B, a remarkable symmetry will be observed in the arrangement of the lateral members. Applying the terms "node" and "internode" for convenience only, it will be noticed that the fourth leaf and branch (l^4 b^4,) through the growth of the internode next forward have been separated from the terminal bud, which has freed itself by pushing forward out of the sheath of the fourth leaf. The branch does not even in the bud occupy the axil of this leaf, and at present can be seen supra-axillary, much separated, and also about to free itself from the sheathing fourth leaf. The growth of the internode also exposes the epaulette of eight minute roots (r^4) in a double row on the shoulder of the rhizome, just below the next or fifth leaf, and on the opposite side from, but above the fourth branch, (b^4). The number of the roots is either eight or six in each epaulette, in all the plants seen, and the older are furnished with branched rhizoids. Throughout, the protective precautions will be found remarkable. The earliest sheath (l^1) envelops all the younger members of the rootstock forward, l^2, l^3 performing successively the same office. In addition to this cumulative sheathing, the thick midrib of each leaf-sheath will be found directly over the enclosed branch-bud it immediately protects. As the rhizoma develops, every young lateral member in the manner above described frees itself from the mummy-like wrappings, one by one, and takes its place in the plant community. It will be observed that the arrangement of the roots, branch and leaf is alternately reversed in each succeeding internode, the cartilaginous roots alternating with

the branch, affording at once an even support in the sand or on the rock, and balance in the water, very complete and effective as a mechanical arrangement calculated to resist great strain.

Zostera, accustomed for the most part to protected waters and more or less muddy bottom, has numerous weak roots in irregularly placed cushions, and the more fragile leaves exhibit no especially effective means of bud-protection.

The fibro-vascular bundle-traces (C^2) show that the leaf-trace, and the root-trace in the "internode" behind it arise from nearly the same plane and simultaneously, the leaf and roots themselves never being far separated when mature. The bundle-trace to the branch has a very different origin, and at no time appears axillary. In the older parts of the rhizoma there are three fibro-vascular traces (the vascular system weakly developed), but the lateral ones are not in a plane with the branches and roots. At each branching of the central trace, however, toward the leaf or roots the lateral traces send in to its support tributary horizontal branches.

The leaves, mostly from sterile branches, are numerous, slender, smooth, coriaceous, dark-green, from one to two and one-half millimeters in width, oval in cross-section, and usually from one to two and one-half meters long. They are provided with sheaths from ten to thirty centimeters or more in length, opening at the side and ending in short, rounded stipules. The numerous small nerves of the sheath are resolved above into three, which continue through the length of the long lamina to near its two-lobed extremity. At intervals there are simple cross-veinlets. The extremities of the young and still enclosed leaves are beautiful objects, from the development of the ruffs of "fin-cells," transparent, of various forms, and arising from the leaf a little within the margins (Fig. K). These persist after the leaf is free in the water. Similar structures are known in species of a few related genera.

The slender (one to two millimeters in width) flowering stems, are from lateral branches, and are concealed and protected by the more distal leaves of the leaders. They are

quite leafy at the base, and rise from one-third to two-thirds of a meter, to the summit of the upper spathes, and by means of the extension of the leafy tips of leaves, spathes and spathe-sheathes, are continued to the height of a meter or more. In the stem are from three to five nodes with sheathing leaves, one or two of the lower leaf-sheaths usually empty. The upper are occupied by the clusters or branches of spathes. The uppermost cluster, however, terminates the stem, and usually has no sheathing leaf corresponding to those of the nodes proper, its place being taken by the lower spathe-sheath. The stems of staminate plants are usually shorter than those of the pistillate; and instead of two or three spathes in a cluster, there are usually three or four shorter ones in the staminate plant. The pistillate inflorescence is carefully shown in Plate I, A, and apparently this arrangement is repeated, in both sexes, in all cases. The arrangement of spathes and spathe-sheaths is the same as in Zostera, except there is no prolongation to the axis of the branch bearing them. From their beginnings the buds and the sexual organs are provided with a remarkable system of shields. Referring to figures A and C[1] we shall find retinacula, spathe, spathe-sheath, successively embracing the members within, and the whole, as well as the other branches above it, enclosed by the strong sheath of the nodal leaf.

As the various sheaths burst because of the expansion of the growing parts within, the flat, broad, shredded remnant is seen, characteristic of the older leaves of Phyllospadix.

The spathe proper and its spadix are sessile on a flattened, common peduncle, two to three centimeters long. Reference to the figures D and E will show the flattened staminate spadix, the oblique arrangement in two rows of the pairs of sessile, distinct anther-lobes, (each pair a single "two-celled" anther), protected by the broadly ovate, somewhat falcate, obtuse retinacula or appendages; also the young pistils in two rows on the pistillate spadix, their retinacula oblong and obtuse.

But we must here state at length several additional facts which appear never to have been recorded, and correct a few important errors.

In anthesis the staminate retinacula, firm, chartaceous, overlapping laminæ, lift, then recurve one by one, only as the individual anthers mature (Fig. D). They push off in this process the spathe, and neither ever returns to the original position, as their protective function of course ceases with the discharge of the pollen. The cells of the outer epidermis of an appendage at the line of flexure are longer and thinner than the adjacent ones, and those of the inner epidermis are shorter and thicker walled. Presumably an increase of cells takes place among the latter at anthesis.

The stigmas, only, of the young pistils are extruded at maturity (Fig. A). The spathe and retinacula closely invest them, until by the growth of the fruit and the curvature of the old spadix (Fig. E) the whole is carried out of the spathe. But at no time is there a reflexing of the pistillate retinacula, although Ruprecht's figures and some descriptive statements assert the contrary.

An interesting fact developed is the presence on the pistillate spadix, alternating with the pistils, of pairs of rudimentary anther lobes whose lower part is sufficiently developed to produce even a few pollens, the upper portion remaining an undeveloped cellulose point (Fig. G). No pollen is apparently discharged, however. If these anthers had been fully developed we should have precisely the arrangement and appearance of the monœcious spadix of Zostera.

In Zostera, apparently the older genus, there is a curved ridge connecting the twin anther-lobes in their younger stages. This is believed by Hofmeister and subsequent observers to be a "connective," and as each of the two lobes has the two pollen-sacs or loculi of the ordinary anther-lobe, the two lobes together form one quadrilocular anther, which appears on the Zostera spadix alternating with the single pistil. The rudimentary anthers on the pistillate spadix of Phyllospadix are connected throughout their whole existence with exactly such a curved ridge, shown in figure G. On the staminate spadix, however, this connection is scarcely traceable, even when the anther is very young, and when it is mature the connective seems to have disappeared.

That these rudiments have a normal origin is seen in G, (left hand fig.), a drawing from sections of the young pistils and anthers where the latter appear to be as well-formed at this stage as the ovaries. The number of anthers on a well-developed staminate spadix is usually twenty or twenty-two, (forty to forty-four lobes), the number on the rudimentary ones on a similar pistillate spadix is about twenty, the pistils eighteen or twenty, showing that on the staminate spadix anthers have not developed in place of pistils; on the contrary, I have not been able to find the least trace of a rudimentary pistil either on the young or the mature staminate spadix.

From this evidence, the derivation of one genus from the other seems undoubted; also it would appear that the staminate spadix, and consequently the diœcious condition of the genus had taken on a very decided character, and had probably been brought about in recent geologic times, if we are to judge by the persistence and character of the rudimentary organs.

In structure, the anthers have been described by Bentham and Hooker and others as "like Zostera." The rudimentary organs with their connective enable us to prove this assertion, the pair, as in Zostera,* constituting but a single anther. Sections of Phyllospadix anthers (Fig. J) also show that each lobe has two pollen-sacs similar in appearance to those seen in sections of the anther-lobes of our Pacific coast Zostera. In one respect they differ, however. In Zostera the

* A curious confusion in the description of Zostera anthers appears in all the standard systematic works in England and America, viz., in Bentham and Hooker, Gray's Manual, and Watson's Bot. of Cal. The anther is described as "one" and "one-celled"—a manifest contradiction. If the anthers are single, between pistils, then they are not one-celled. If they are one-celled, then what we have termed anther-lobes must be considered as two anthers. Eickler in "Blüthendiagramme," and Ascherson in "Die Pflanzenfamilien," give a lucid and perfectly correct diagnosis of the anther. Bentham and Hooker say of Phyllospadix also, "anthera . . . . 1-locularis," which may have led Mr. Morong, even so late as the current year (1893), into the statement, (Naiadaceæ of the U. S.), that Phyllospadix has "numerous sessile stamens in two rows . . . 1-celled."

wall between the sacs disappears at the dehiscence of the lobe, after the usual mode in anther-lobes in quadrilocular anthers, and leaves the lobe "1-celled," as the phrase is. But in all the Phyllospadix examined, the dividing cellulose wall, after the discharge of the pollen, is left as a firm membrane (Fig. D, a). This gives somewhat greater protection to the pollen, no doubt, than the more fragile wall found in Zostera.

While at the Hopkins Seaside Laboratory, I was enabled to investigate the anther dehiscence and the probable mode of pollination. This was done by means of the sea-water tanks, as well as observations along the shores of Monterey Bay. The alternating low-tides on this coast are known as the "large" and "small". The "large" tides at the change of the moon often leave Phyllospadix uncovered; but at such times these tides do not occur when the sun is much above the horizon, so there is little chance of leaves or flowers being destroyed, as they would be if exposed to the air and sunlight at the same time. The staminate plants are much less numerous than the pistillate. In the localities most favorable for the Ph. Torreyi flowers, the proportion of staminate to pistillate was about one to twelve. In more exposed situations staminate plants were much rarer, and on much exposed shores pistils of Ph. Scouleri* often fail to be fertilized,—perhaps not wholly on account of the scarcity of the staminate plant, for the violence of the surf no doubt disperses and destroys the pollen to a greater extent than in quieter places. The staminate plants, according to my experience, occur more inshore; the pistillate plants are all about them, extending also into deeper water.

After the anthers with partially reflexed retinacula have been exposed to the air for a time in the low early-morning tide, or have remained in the comparatively quiet shallow slack-water of the ebb, they will open more readily, with the

*Hooker's erroneous figure showing an ovoid pistil (Flora Bor. Amer. II, t. 186.) may have been based on a specimen with unfertilized withered ovaries. His "capitate stigma" is the tip of a style from which the stigmas have fallen.

accession and quickened movement of the earlier waves of the flood. The anther opens near its lower obtuse end, rips upward along the depressed median line with a quick movement, and exposes the numerous pollen filaments, lying parallel and obliquely placed in each pollen-sac. The masses are white, silky, and appear somewhat spirally twisted. The slow advance and recession and the sudden lashing of the swell carry the long locks of sea-grass with them, throwing the spadices back and forth, and dragging them roughly on one another and on the leaves.

The pollens average 1 millimeter in length by .004 to .005 of a millimeter in breadth. They are slightly flattened and broadened at the extremity (Fig. D., pn.), and some are enlarged toward the middle. Each pollen filament when first exposed is protected by a layer of air, and a cluster of them loosened from the pollen sac springs immediately to the surface of the water, while the filaments repel one another sufficiently to form at once a silvery arachnoid film, perhaps a centimeter across. These are never abundant, but they float hither and thither with the water, and among the doubling and swinging pistillate plants. At the lowest stages of the tide the films of pollen could easily be thrown upon the half-exposed pistillate spadices, and would adhere to the protruded stigmas, as they were observed to do in the aquarium. Unquestionably this is one mode of pollination.

When the pollen has been exposed for hours in the open sac, it does not necessarily rise to the surface but floats in the water where it can be more readily carried to the usually submerged stigmas. Clavand, (Actes d. l. S. Linn. d. Bordeaux, T. II, 1878,) describes this as the mode of transference in Zostera marina, and mentions no others; but the young pollens of the Pacific coast Zostera spring to the surface, exactly as do those of Phyllospadix. I have examined microscopically both the floating and the submerged pollens of Phyllospadix, taken in the conditions above described, and found in both the natural streaming of the protoplasm. Both would presumably be capable of effecting impregnation at the time. The protoplasm was observed streaming in a filament

taken from an anther three days open, and they may possibly live a much longer time in the open sea.

The stigmas are described as capillary by most authors excepting Ascherson. They are ovate lanceolate, acuminate, thin, irregularly lobed and laciniate.

The nucleus of the single, orthotropous, pendulous seed, enclosed in a strong double testa, is carinate dorsally, somewhat compressed, and presents, like all the forms related to it, a largely developed hypocotyl with no surrounding endosperm. The hypocotyl has two lateral fleshy lobes folded toward the cotyledon (Fig. H). The narrow cotyledon, two millimeters long, is tubular and two-lipped, the posterior lip two-lobed and shorter. Enveloped by the cotyledon are two to four alternately shorter flat laminæ, obcordate or roundish, the first leaves of the plumule (H, lower fig.).

In various places we have referred to the bearing of peculiar morphological features upon the generic characters of Phyllospadix. We now turn to the anatomy of the vegetative organs.

The rhizoma has marked provisions for clinging to a hard substratum, but in itself is brittle and weak. The leaves and stems are correspondingly strong and flexible, the root firm and resistant.

The rhizoma is almost wholly a mass of parenchyma. Of the three bundle-traces the middle one only shows a few poorly developed annular, reticulated or dotted vessels, some weak libriform cells, and no strong wood fibres. Sclerenchyma fibres are wholly wanting. Indeed, the only strengthening tissue in the rhizoma is collenchyma-like cells appearing in a few rows in the cortex.

Turning to the figures of the root-sections (R), it will be seen that the firmness in the root is due to the broad sheath of epidermal and hypodermal cells with remarkably thickened walls, the parenchyma of the middle region remaining thin-walled.

Figure L, shows a transection of the leaf of Ph. Torreyi near the epidermis; and M, (lower fig.) transections of a por-

tion of the stem of Ph. Scouleri. The stem and the leaf we have found bear the brunt of the surf; and underneath the thick chlorophyllous epidermis, destitute of stomates, both members show large areas of strong sclerenchyma fibres (sc.), each fibre several millimeters long and of surprising strength. In the flat leaf of Ph. Scouleri, the entire margin of the leaf beneath the epidermis is a steely strand of sclerenchyma, and the remaining tissues are well armored with it. Schwendener's demonstration in "Das Mechanische Princip," that the sclerenchyma is the prime factor in the strengthening apparatus of a plant could find no better illustration. For after the old leaves are beaten to pieces by the tremendous surf these fibres long remain at the base. Bold shore specimens can be recognized in herbaria from the numerous bristle-like strands of sclerenchyma remaining at the base of the stems.

The longi- and transections under M, of a stem fibro-vascular bundle, illustrates its simple and feeble structure.

Zostera leaves, even those of our large coast species, show large lacunæ and no sclerenchyma fibres whatever, in the specimens examined. The stems are relatively no stronger. These Monterey Bay Zosteras, although in open water are subjected to no such impact as the plants growing in the surf. It is only in the rhizoma, where there are scattered strands of sclerenchyma, that we find a member stronger than in Phyllospadix, the roots being without strengthening elements, as Sauvaugeau has demonstrated those of Zostera marina to be.

Aside from correcting certain errors this structural study has brought out two salient facts: First, the genus Phyllospadix, not yet found fossil, so far as we know, is probably an offshoot and apparently a recent one, from the much older genus. The presence of the now quite useless but still well-marked rudimentary male organs on the pistillate spadix, which present us with an inflorescence identical in plan with that of Zostera, is offered as evidence of this; while the separation of the sexes, on male and female plants, indicates a differentiation in advance of the original monœcious arrangement still adhered to in the last-named genus, and shows the vigor of

the later type. Second, the conditions in which the ancestors of Phyllospadix, on this coast, found themselves, have forced, in the growth of the genus, the development of an unusually strong stereome, or system of strengthening cells in stem and leaf, to which Zostera has no tissue which will bear any comparison, and a symmetrically balanced rhizoma with a remarkable system of shields and sheathing members, designed to protect the buds and young reproductive organs.

In the morphology and anatomy of a plant, I believe we may find at least a partial record of the influences of past environment in the struggle of the organism, not only for existence, but for upward development;—*i. e.*, for a mode of living which will make the best use of the resources at its command. In its present environment, if likely to have been long continued, we may find still further explanation and corroboration of the structural evidence. In looking for the causes which lead to the evolution of a new genus we may profitably consider a similar line of evidence, adding the testimony to be derived from geographical changes and geological records.

We have already sufficiently explained the present habitat of Phyllospadix, on stony and rocky shores, and connected its peculiar structure with the supposed effort on the part of the organism to meet the conditions (for a plant) of an unusually stirring existence. But why a branch of the shallow-water Zosteras should have ventured on this bold career, and what the conditions really were during its earlier years, cannot perhaps be more than imperfectly answered, in the present state of our knowledge.

Referring again to the distribution of living sea-grasses, and leaving out of account the two Zosteras of wide distribution, and the few doubtful species and stations, we find there are certain geographical centers of development. And we may suppose these regions to have preserved something in their conditions, at least not unfavorable to the continuance, and even favorable to the further development of the old geologic types. They are grouped as follows:

Australian shores, (inc. 1 Malayan form), 15 species.
[Eight of the above extend westwardly along the Indian Ocean shores to the Red Sea and down the E. African coast region, where appears one additional species]
The Antilles, (including Key West), . . . 5 species.
Pacific North America, ... 3 "
The Mediterranean,* . . . . . 2 "

Not attempting here to account for the discontinuousness of these areas, we call attention to the fact that the principal center named,—Australia,—is a region where an unusually large number of the Eocene types of land plants are found living, preserved no doubt through absence of violent change in conditions. Similarly a conspicuous number of Miocene and Pleiocene forms are represented in the present Western North America Flora. These facts in a broad way may have their significance; and, as bearing upon the question, we may be allowed to refer,—in connection with the present uniform aerial temperature of California, accompanied by a surface marine temperature which does not vary 10° in the year at the Golden Gate,†—to the universally accepted belief that a uniform sub-tropical or warm, temperate climate existed around the whole North Temperate and a portion of the Arctic zones through long periods of the Tertiary, especially of the Eocene and the Miocene, times contemporary with supposed geologic remains of the early Zosteræ.

But while the old races have been continued on this coast, there have been causes at work which have brought about the vigorous and remarkable divergence seen in the varying forms of our genus and in the robust open-water Zostera of the Pacific coast. This coast is geologically new. Dana asserts that the Sierras were lifted in the middle of the Mesozoic, preceding the Cretaceous, experiencing great subsequent elevation; also that the coast ranges date their emergence from various peri-

*This table is constructed from stations vouched for in Ascherson's various papers, and slightly modified by later information.

† According to Professor Davidson's observations on marine temperatures, 1874 to 1883.

ods in the Tertiary. Distinguished later authorities maintain that much of the coast range region is of recent appearance, and that it has undergone great vertical oscillations during recent times. The remarkably bold shore of California may be due to the above phase of its geological history. Ten miles off the coast the ocean shows an average depth of 100 fathoms. But from the brink of this narrow submarine terrace, the bottom rapidly descends to 2,000 fathoms or more, the 1,000 fathoms line being on the average only 50 miles off shore. Submarine valleys and cañons of great depth, testifying to some great subsidence, often cut through the usual terrace-barriers, into the very shore line itself; such is the case at Monterey Bay. The bottom temperature 1,000 fathoms off the coast is 35° Fahr., or but little above freezing. The winter surface temperature at the Golden Gate is about 50°, the summer temperature less than 60°. In the most sheltered parts of Monterey Bay, near Monterey, the summer temperature is about 60°, while on the more exposed shores it has been found at times to be below 50°.

There is no shallow, shelving sea, as along the old and long worn Atlantic slope of the United states, and few long bays or shallow estuaries and sounds, whose temperature is greatly elevated during hot summers or depressed during cold winters, and which easily mingle their waters with the open ocean. On the contrary, on a coast rapidly descending to great and cold depths washed by a current from the north, are flung with great force waters of an even but low temperature, lower still, perhaps, in the vicinity of the submarine valleys. These beat upon the coast and upon the littoral plants with great force. Not alone in the furious storms of the rainy season is the whole coast-line subjected to their powerful action,—even during the long, stormless summers, the breakers are undoubtedly greater in size and the movement of the water everywhere stronger than on the Atlantic coast in similar weather.

In these conditions the marine plants of the eastern Pacific seem to revel. Gigantic fucoids, robust red-algæ, strong pliant Zosteræ, all attain a completer physical development,

perhaps, than in any other waters. Possessing the favoring influence of annual uniformity, presumably for an enormous number of years, the apparent rigors of the sea not improbably have acted as a stimulus to the races strong enough to enter its theatre of action. Not improbably the plastic organism of Phyllospadix, subject to forces long continued, inflexible, and dynamically great, has not only developed a structural system so resistant and perfect as to welcome these remarkable conditions, but, like the builders of the coral reef, it can no longer thrive except in the surf or within the influence of the titanic movement of the open ocean.

I am told that the marine deposits in the coast ranges have not been sufficiently studied to enable specialists to outline clearly the conditions prevailing on the east Pacific shores through the Tertiary and the Quaternary. No question like the present one can approach a settlement until the facts obtainable from geological sources are recorded.

On the other hand, it can safely be said that the biological evidence is likely to favor the hypothesis of a very long period of uniformity in temperature and in the character of the ocean shores and currents, if not in the shore lines, along the whole California coast. It is impossible at present to indicate its duration, but it may well have existed from early in the Quaternary, perhaps even from the confines of the Tertiary, down to present times.

PALO ALTO, CAL.,
Sept., 1893.

EXPLANATION OF PLATES.

PHYLLOSPADIX, PLATE I.

A :—Stem from pistillate plant (Ph. Torreyi), × ½. *r—l*, bases of radical leaves ; l^0, cauline leaf with empty sheath ; l^1, l^2, first and second leaves with axillary spadices ; the old leaf-sheaths are spread open. I and II, the first and second flowering clusters, with internode and subtending leaf. III, third flowering cluster, terminating the stem, with no subtending leaf, its earliest spathe on the same side as the earliest in II, thereby securing in the bud, the protection of l^2. sh^1, spathe-sheath enclosing sp^1, the lower spathe and spadix. sh^2, second spathe-sheath, enclosing sp^2, the second spathe and spadix.

B :—Rhizoma, (natural size). *r. l. b.*, roots, leaf, and branch, numbered through four successive "internodes." The oldest set of roots has rhizoids with adhering sand.

C^1 :—Diagram ; transection of a pistillate stem, in the bud ; lettered as in A. *sx*, spadix.

C^2 :—Diagram ; longisection of rhizoma, in the bud ; lettered as in B.

D :—(1) Staminate spadix, at anthesis, (natural size). *rn*, retinacula or appendages ; *sp*, spathe ; *a*, anther-lobes.
(2) An open anther-lobe, × 3, showing the median membrane.
(3) A few pollens, arranged as seen in pollen-sac.
(4) Apices of three pollens (at right), × ~~500~~ 350

E :—(1) Pistillate spadix (Ph. Scouleri), mature, (natural size). *sp*, spathe ; *sx*, spadix ; *l*, remains of spathe-sheath, remains of a leaf seen below. The retinacula, *rn*, partly conceal the mature fruits.
(2) Above, *fr*, a single fruit (Ph. Scouleri), front view, × 2.
(3) Same in section, (at the left), showing the point of attachment, and the pendulous seed.

F :—Young pistil (Ph. Torreyi), with stigmas, × 3.

PHYLLOSPADIX, PLATE II.

G :—The rudimentary male organs (Ph. Torreyi).
(1) On the right, spadix, *sx*, with one partly mature pistil, circular scars where two have been removed, and above, several small ovaries, *ov.*, each with retinaculum, *rn*. Pairs of rudimentary anther-lobes (joined by the curved connective), alternate with pistils, × 3.
(2) On the left, a section of very young pistillate spadix, × ~~120~~ 50 ; *ov.*, ovary ; *a*, anther lobes ; *rn*, retinacula. The elevation under the anther-lobes is the connective ridge.

H :—(1) Embryo of mature seed (Ph. Scouleri), × 5.
(2) The same in longisection ; *hyp.*, winged hypocotyl ; *cot.*, cotyledon, inside the first leaves of young plant.

J :—Diagram ; transection of young anthers on staminate spadix (Ph. Torreyi), showing wall between pollen sacs.

K :—" Fin-cells " near the margin and tip of a very young leaf, × ~~120~~ 50.

L :—Transection of leaf (Ph. Torreyi), showing epidermis ; areas of sclerenchyma cells, *sc*, and parenchyma, × ~~600~~. 300

M :—Stem (Ph. Torreyi), × ~~600~~. 300

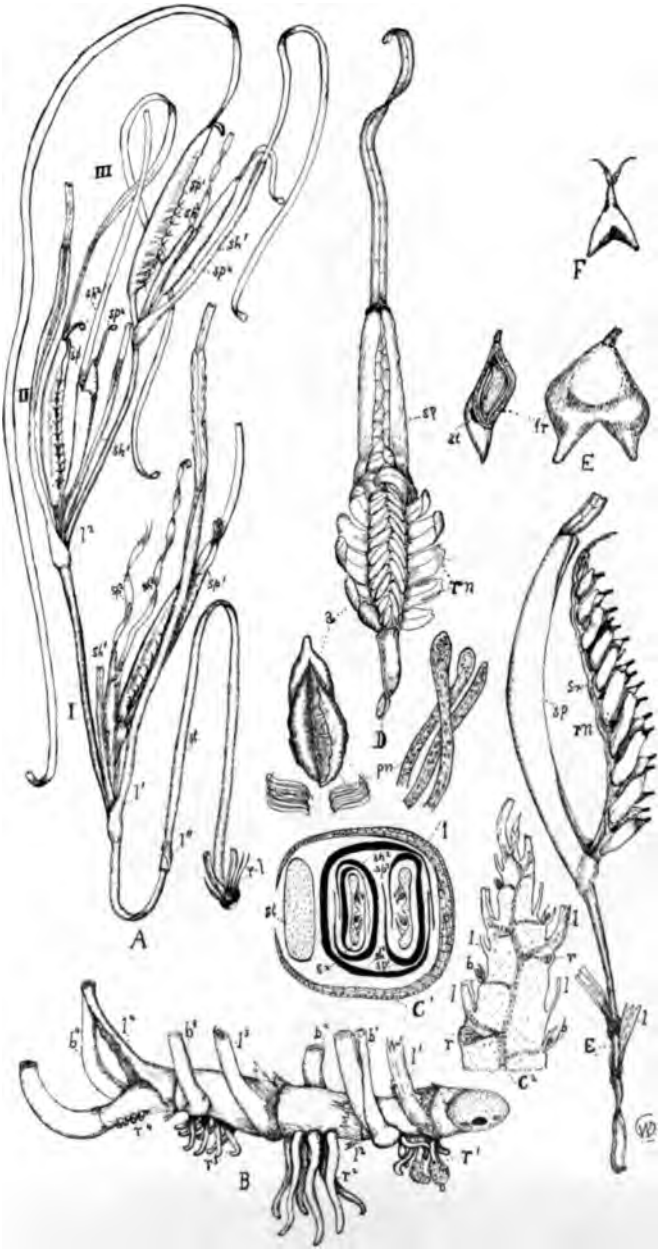
(1) *f-v-b*, fibro vascular bundle in transection, surrounded by an endodermis.

(2) Longisection of same, showing annular spiral vessels, soft bast, and parenchyma.

(3) Below, a transection of stem near the epidermis, the large areas of sclerenchyma, *sc.*

(4) Single sclerenchyma fibre, *sc.*, surface view.

R :—Transection of root (Ph. Torreyi), near epidermis, *ep* ; sheath of strong, thick-walled hypodermal cells below, × ~~600~~. 300


A
B
C
C'
D
E
F
I
II
III

PAIR OF LAKE LAMPREYS FROM THE SAME NEST.

THE LAKE AND BROOK LAMPREYS OF NEW YORK, ESPECIALLY THOSE OF CAYUGA AND SENECA LAKES.

By SIMON HENRY GAGE.

If one glances at a topographical map of the State of New York, there will be seen in the western half a remarkable series of long narrow lakes, with a general north and south direction. These lakes occupy a basin between Lake Ontario on the north and a ridge that separates this basin from the Mohawk River on the south-east, and the Susquehanna River and its tributaries on the south. This elevation bordering the lake basin on the east, south and west, and forming nearly a semicircle, is drained to the north into the lakes, and into the Susquehanna and Mohawk Rivers on the south. The area of elevation draining into the Mohawk, and thence to the Hudson River is, however, comparatively slight.

The central and largest of these lakes is Cayuga (Pl. 2), flanked on the west by Seneca, next in size, then come Keuka, or Crooked, and Canandaigua Lakes. On the east are, in order, Owasco, Skaneateles, Onondaga and Oneida Lakes. In addition to these are numerous small lakes or ponds scattered among the large ones. A further study of the map will show that all of these lakes have important tributaries especially at the head. The outlet either flows into one of the larger lakes or directly into a common outlet. The final destination of all the superfluous water is Lake Ontario, through the Oswego River; and thence through the St. Lawrence River it reaches the Atlantic Ocean, 700 to 800 miles to the eastward. With the other great lakes the connection is by the Niagara River, the falls forming, at the present time, an impassible barrier against the passage of fishes from Lake Ontario to the other great lakes.

From these, the present connections, and from the possible connections with the Susquehanna and Hudson rivers at an earlier date, it is to be expected that the aquatic fauna of Cayuga and the other inland lakes would be rich and varied.

By assiduous personal study and observation and the wise direction of students, Professor Wilder has shown that in the Cayuga Lake basin there are 21 families, including 40 genera and 59 species representing the group of fishes.

A further study of the outlets of these lakes, to Lake Ontario and thence to the ocean, reveals the fact that they are long and tortuous, and besides possess many rapids and shallows. These conditions have probably obtained in recent geological time, a time sufficiently great to lead one to expect that the lake forms, especially those that had ceased to be migratory, would have received a certain stamp or impress from the special and somewhat isolated environment. Furthermore, migratory or anadromous forms, in bodies of water like these, where they are surrounded by plentiful food, might gradually become less migratory and as the difficulties of reaching the ocean were increased by changes in the character of the outlet or the gradual recession of the ocean, they might finally remain permanently in the fresh inland waters, and like the other permanent inhabitants be modified by the special environment.

The more this lake fauna is studied the clearer does the local coloring, so to speak, appear. Among the lampreys, the subject of this paper, there appears not only the local impress but almost positive evidence that forms, at one time naturally passing their adult life in the ocean, have become accustomed to remain permanently in fresh water with corresponding changes in the more impressionable or less important parts. I say more impressionable, for it is one of the fruits of modern research, in the light of evolution, that the most fundamental organic structures, having to do with the mere existence of an organism without regard to its upward progress, are more persistent and less changeable than less ancient and less important organs, that is, less important from the mere existence standpoint.

Problems having a philosophical bearing have always been the most fascinating to the natural philosopher as well as to the metaphysician. In the study of living organisms this has been especially true since the doctrine of evolution has so profoundly influenced thinking men. Naturally therefore, Professor Wilder, who came to his professorship in Cornell University—which itself was making a leap in educational evolution—during the time when evolution and various collateral hypotheses were in the fiercest conflict with all previous doctrines, theological and otherwise—naturally Professor Wilder turned with especial interest to the study of the Cayuga Lake fauna which promised information concerning the effect of local environment, and change from preceding conditions. Naturally also he turned with especial interest to the lamprey, the lowest representative of the vertebrates found in the lake fauna.

This interest was transmitted to his pupils, and since 1875 the writer of this article has lost no opportunity of studying the lampreys at all stages of life, and this study has been devoted to the living animals rather than to the dead organisms, although the understanding of their activities and physiological functions has been constantly clarified by experiment and anatomical study.

Characterized zoologically the lampreys (Petromyzontidæ) are fish like vertebrates, with an eel- or snake-like form and a metamorphosis, comparable to that of frogs and toads. The skeleton is wholly cartilaginous and the notochord persistent. Neither pectoral nor pelvic limbs nor their arches are present although the dorsal and caudal fins are well developed. The branchiæ are extended, and open by seven independent openings on each side, and in the adult the gills are pouched (whence the name Marsipobranchii sometimes used). The nasal sac is single and blind and opens to the exterior by a raised papilla on the dorsimeson just cephalad of the median, or pineal, eye and of the paired eyes. Apparently no jaws are present and the mouth in the adult is suctorial and armed with horny teeth; but the rudiments of jaws have been shown by Huxley and others to exist. The tongue is a piston-like rasp in the adult, absent or rudimentary in the larva.

According to all zoologists the lampreys (Petromyzontidæ) are very low in the zoological scale, and according to many they are degraded forms. They are found in the temperate regions of both the northern and southern hemispheres; and all, so far as investigated, lay their eggs in fresh water and pass their larval life there. Some pass their entire life in fresh water while others go down to the sea, but all finally, on the attainment of sexual maturity, once more ascend the streams to their birth-place where the eggs for a new generation are deposited, thus completing the life cycle.

Both the lake and the brook lamprey agree entirely with the designation for the Petromyzontidae as given above, and besides the lake lamprey agrees with the characters given for the genus Petromyzon, viz.: The supraoral lamina, or maxillary tooth-plate, is contracted and with two cusps placed close together; infraoral lamina or ~~maxillary~~ tooth-plate with six to nine cusps. The discal teeth are in concentric series; those on each side of the mouth are bicuspid. (Pl. VI).

With reference to the specific relationship of the large lake lamprey there has been considerable diversity of opinion. Up to the year 1875, the University had only secured small lampreys caught on fish, none of them exceeding 15 to 20 centimeters. The coloration of these lampreys was white on the ventral half and nearly uniformly black, or bluish black along the dorsal half of the body. In the spring of 1875, however, there was obtained from Cascadilla Creek, near the University, a specimen nearly twice as large as the ones usually obtained and with a strikingly different general appearance, due in part to the greater size and more variegated coloration, but mostly to a large rope-like ridge extending along the back from the gills to the dorsal fin. The two dorsal fins were continuous, simply having a depression between them. The specimen was photographed when fresh and is reproduced in Pl. III, fig. 5. The general appearance, so strikingly unlike either the small lake lampreys previously obtained or the specimens of true sea lampreys in the museum, seemed to indicate that, responding to its special lacustrine environment this lamprey had assumed characters which

might be considered generic or at least specific; and Professor Wilder suggested to his special class, before which the specimen was brought for study and comparison, that if the peculiarities noted in this first specimen were found constant and characteristic of the lake lamprey one might consider it a distinct species at least and give it the specific designation of *Petromyzon dorsatus*, from the dorsal ridge. But believing that the admonition to "prove all things and hold fast that which is good" should be followed in science as well as in philosophy, publication was reserved until other specimens could be obtained to show whether the first was typical or a mere sport or transient variation from the truly typical form.

It fell to the writer, then student assistant to Professor Wilder, to prosecute the search for other examples of the lake lamprey and to aid in the final solution of its life history and systematic relationship, the work being constantly forwarded by the advice and encouragement of Professor Wilder, as well as by the freest use of his personal notes and drawings.

In prosecuting the investigation almost no aid was obtained from the lake fishermen. All they knew about the lampreys was that they were sometimes caught clinging to other fishes. One man, however, living near the inlet, brought to the laboratory six larvæ and stated how they were obtained. He also said that the large ones went up the inlet in the early spring. By diligent inquiry of people living near the inlet, information was obtained so that in the spring of 1876 the explorations of the inlet were successful and the adult ones were found spawning, and the larvæ were found in the sand banks along the edges of the stream. Of the seven large lake lampreys caught, five possessed the dorsal ridge so characteristic of the first one obtained. Upon dissection it was found that the ridged ones were males and those without the ridge females, so that from this time on it was exceedingly easy to determine the sexes in fresh specimens by this feature alone. Alcoholic specimens which had been caught in the breeding season were far less easily separated into the two sexes by this sign since the body was badly shrunken in alcohol, and the females so preserved often appeared to have nearly as large a ridge as the males. In

1878–1879 specimens were submitted to Prof. D. S. Jordan, who designated the lake lamprey as *Petromyzon nigricans* of Leseur in the synopsis of the fishes of North America ('82), remarking: "It is possibly only a variety of *P. marinus*."

During the college year, 1885–86, S. E. Meek, one of Professor Jordan's students, as fellow in zoology in Cornell University, made a special study of the fishes of the Cayuga Lake basin; and from the interest already aroused in the lampreys of the lake, he joined the writer, during the spring of 1886, in a critical and extended examination of the lake lampreys. Nearly 800 specimens were studied, especially as to external sexual characters and specific relationships. In a joint communication before the American Association for the Advancement of Science (Gage and Meek, '86) the following points were presented: (a), "The determination of the specific identity of the large Cayuga Lake lamprey and the sea lamprey; (b), The determination of the constant presence of a dorsal fold or ridge in the males and of a ventral fin-like fold in the females of [the Cayuga Lake] *Petromyzon marinus*, at the breeding season."

Jordan and Fordice ('85), in "a review of the North American species of Petromyzontidæ," remark concerning the Cayuga Lake lamprey. "We have examined marine examples of this species [*P. marinus*,] and also numerous specimens in all stages of growth from the larva to the adult form, collected by Dr. Burt G. Wilder, in Cayuga Lake, at Ithaca, N. Y. Among these are types of *Petromyzon dorsatus* Wilder, which seems to be merely a land-locked form, not permanently distinct from *P. marinus*. The characters assumed to distinguish this form from the true *marinus* are, however, more or less inconstant and not of specific value."

Even after the extended study of the 800 specimens mentioned above, there still remained to be settled the question whether or not the external sexual characters of the dorsal ridge in the male and the anal fin-like structure in the female were constant throughout the year or merely seasonal characters comparable to so many others known in the animal world. There was also the query whether the American,

true, anadromous sea lamprey developed the peculiarities found in the lake lampreys at the spawning season, and according to Seeley ('86) also present in the European marine lamprey during the breeding season.* Until these questions could be satisfactorily answered there would remain doubt as to the really constant peculiarities developed in the lake form. During the winters of 1875 and 1877 large lake lampreys were obtained of both sexes, and concerning them the notes either say "no ridge" or "ridge very low and broad," so that additional information must be sought. In the autumn and winter of 1886–87 great inducements were offered to the lake fishermen to obtain large lampreys. During that winter and since then throughout the year, large specimens were obtained and brought to the University. All of these large specimens looked alike. There was no dorsal ridge in any of them nor was there an anal fin or projecting urogenital papilla in any of them, and the two dorsals were well separated in all (Pl. III, fig. 6). It was only on dissection that the sexes could be distinguished. Thus it was definitely determined during the autumn and winter of 1886–87, that it was only during the spawning season that the special external sexual characters appeared in the lake lamprey.

In answer to the second query concerning like seasonal peculiarities in the true marine lamprey: alcoholic specimens obtained at various seasons were examined, but as stated above, whether or not a ridge was present during life is not easy to determine from alcoholic specimens. So that while ridges appeared on some of them, it was found by dissection that the animals were in some cases males, but quite as often females. Uncertainty must therefore continue until a considerable number of fresh specimens could be examined. This was made possible by the intelligent aid given by Mr. Thomas S. Holmes, of Lawrence, Mass., who sent specimens of the marine lamprey which were running up the Merrimac River to spawn. The specimens were usually sent in the early or middle part

* During the month of August, 1889, the writer saw in the aquarium of the Trocadaro in Paris several large marine lampreys, some of which possessed very prominent dorsal ridges.

of June, that is, in the height of the running season. Some males exhibited a ridge, but many none, so that it was not possible to distinguish the sexes with certainty by the external appearance.

In 1893 it was found that a fully mature lake lamprey obtained April 10, that is about fifty days before the time for spawning, showed none of the seasonal characters, and hence it seemed likely as the spawning grounds of the true marine lampreys were so far from the ocean, that some might set out on their journey to them before any special, external sexual characters appeared. To determine this, Mr. Holmes was asked to secure the first lampreys that should be found running up the Merrimac, and also some at the very close of the season. This was done during the present year (1893). Those caught about May 20, were found without either ridge or anal fin, and the sexes could not be distinguished by any external feature. On dissection, the sexual products were found to be still firmly imbedded in the ovary and testis, or spermary, and in many of them the alimentary canal was large, showing little or no signs of atrophy, except at the terminal part. On July 8, there were received four specimens. Only two were seen by Mr. Holmes after these were caught so that those sent were among the last to ascend the stream. These showed in an unmistakable manner the external characters so striking in the two sexes of the spawning lake lamprey, viz., a ridge extending from the gills to the dorsal fin in the male and an anal fin-like crest in the female. In both sexes the sexual products were partly shed into the abdominal cavity.

Information from the spawning grounds at the head waters the Merrimac River in New Hampshire, shows that the dorsal ridge has been noticed by those familiar with the lampreys in that region.

The dorsal fins in the male especially, are in some cases considerably approximated, but in only a few cases have the marine lampreys shown an appearance of continuity of the two dorsals.

It thus appears that the peculiarities so striking in the first

lake lamprey obtained, are present in the males only, and are seasonal and very temporary. Furthermore, in addition to the characters mentioned above as common to the sea and the lake lamprey, the determination that in the true marine lampreys similar sexual peculiarities occur at the breeding season, removes the last element of doubt as to the very close relationship of the lacustrine and marine forms.

With reference to the specific identity of the lake and the marine lamprey, it seems impossible to doubt that they were originally identical, and that the lake lamprey in its somewhat isolated, inland home has become considerably modified. The most salient and important modifications relate almost wholly to the adult form so far as is known; for the larvæ of the sea lamprey from the Susquehanna River agree so closely with those of the lake that if several living or similarly preserved specimens of about the same size from each locality were mingled, it would be difficult or quite impossible to again separate them. This argument may not be of great importance, however, for as it will be shown later, no definite distinctions between the larvæ of the lake and of the brook lamprey have yet been discovered. The modifications in the adult form are: (a), A very much smaller size for the lake lamprey; the average length in the breeding season being frequently less than half that of the sea lamprey. The dorsal ridge is relatively much more prominent in the male lake lamprey in the breeding season than is that of the sea lamprey, and the two dorsal fins are more nearly fused; likewise the urogenital papilla of the male, the notched appearance at the vent and the anal, fin-like fold in the female are relatively greater in the lake than in the sea lamprey. There is more frequently a larger number (8 to 9,) cusps or teeth to the infra-oral lamina, or the mandibular tooth-plate, in the lake lamprey than in the sea lamprey; and finally there is a greater development of cutaneous pigment and it is more diffusely arranged so that the general coloration of the lake lamprey seems more uniform, and on the whole somewhat darker than with the sea lamprey. Indeed, the marine lamprey is designated by the fishermen as the large spotted lamprey.

Whether these differences, which are mostly of degree, are sufficient to constitute two different species, has been decided in the negative by Jordan, and also by Meek ('82, '85, '88). If the criterion of natural and spontaneous interbreeding be taken to settle the question, it must receive a different answer; for the lake lamprey, from its size alone would not form a mate to the marine lamprey. Of course they are not upon the same spawning grounds, but any one who has watched the spawning of lampreys, (see below under spawning) would, I feel sure, agree with me that the difference in size is so great that even if on the same spawning grounds, they would be mutually incompatible. It is not asserted that it would be impossible to fertilize the ova of a marine lamprey with the zoosperms of a lake lamprey and the reverse, but the criterion of modern systematists is, not possible inter-fertility under very artificial conditions or by the intervention of man, but the natural interbreeding under conditions to which both forms have been subjected for many generations.*

Now while I firmly believe that within comparatively recent times, geologically speaking, the lake lamprey was a true anadromous marine form it seems to me that at present, judged by the physiological test of interbreeding, it would be better to consider the lake lamprey a distinct species, and to designate it either as *Petromyzon unicolor* DeKay, or *P. dorsatus* Wilder, should the Lake Champlain larvæ, upon which

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* For possible readers of this article who have not followed closely the progress of views concerning classification and the nature of "*a species*," it may not be out of place to add that by biologists (this term including both morphologists and systematists) it is believed that "*species*" as an entity in nature, has no existence as was formerly taught, but that the arrangement of closely allied forms into groups or "*species*" is largely for convenience. And as some criterion must be used, the physiological one mentioned above seems to have gained the greatest favor.

As is shown in another article in this volume (J. H. Comstock's), while the practical aim of classification is to subserve convenience, its true purpose is to show the phylogenetic relationships of organisms, and the permanence of any system will depend directly upon the approximation with which this purpose is attained.

DeKay's name was based, prove to be the larvæ of the marine lamprey, which is probable (see Jordan and Fordice, '85, p. 284).

Distribution of the Lake Lamprey.—It is known by personal observation and collecting, to be abundantly present in Cayuga and in Seneca Lakes; and from information obtained concerning the other lakes and from Lake Ontario, it is believed to be present in them also. It is hoped that during the next five years all of these regions can be visited and all the lakes and watercourses of the State investigated to determine the presence of lampreys and their correlation with those now under consideration. It is hoped also to extend the investigation to the Great Lakes and to bring any lampreys there living into the field of comparative observation.

Comparison of the Sexes.—As stated above, except in the spawning season there are no definite external characters by which the sexes can be distinguished. The question then arises as to the necessary steps to make the determination, at any other time than in the spawning season. The only way, so far as is known to the writer, is to resort to dissection. This is the only way also for determining the sex in the larvæ. Upon dissection, even in larvæ 100 milimeters in length, the sexes may be quite readily distinguished by examining the gonads, as the ovary and the ova are markedly larger than the spermary and sperm mother-cells (Pl. VII, fig. 37, 38). The determination of the sexes in large, adult forms is much more difficult. The ovary and spermary are alike single foliated or lobulated organs, and the sperm mother-cells project from the surface of the spermary as do the ova from the ovary, so that from the gross appearance alone, it is not easy to distinguish the two generative glands. When examined as opaque objects, with a lens or with a compound microscope the same difficulty is experienced, but if treated by any of the approved histological methods the true nature of the elements in each case unmistakably appears (Pl. VII, fig. 27 A, 29 A and 28, 30).

After one has become accustomed to distinguish the sexes by dissection, the differences observable by the eye or with a

simple magnifier, are, in most cases, sufficient to make the diagnosis quite certain. In perfectly fresh specimens the spermary is semi-translucent and has a watery appearance, while the ovary is much more opaque owing to the food yolk in the ova. In hardened specimens this difference is lost, however, so that the determination must be made by comparing the size of the gonads, and the relative size of the ova and the sperm mother-cells. The ovary is always larger at the same stage of development than the spermary, and usually the ova are larger than the sperm mother-cells (Pl, VII, fig. 28, 30). If one has but a single specimen or is not accustomed to determine the sexes, the safest way is to make a histological examination.

In plate I, it is seen that the proportions of the sexes are markedly different, apart from the greater slenderness of the female. It was hoped that by a careful comparison of certain definite and easily determined proportions some guide might be found by which the sexes could be distinguished at all seasons and independently of the transient sexual characters at the spawning season. Careful measurements were made of specimens that had been subjected to the same treatment, in fixing and hardening so that the variations due to different reagents should not complicate the problem. Except for the lake lampreys taken in the breeding season where the sexes could be distinguished easily, each specimen measured was sufficiently dissected to determine with absolute certainty the sex. The results of the measurements in all the different forms studied, adult and larval, are given in the following table :

TABLE showing the total length of the lake, the brook, and the sea lamprey and the larva; also the distance in thousandths of the total length from the tip of the oral disc or dorsal lip to the base of the first dorsal fin, and to the vent; also from the vent to the tip of the tail. For the purpose of comparing the total length in the various forms and the proportions of like parts of the body.

THE LAKE LAMPREY IN THE SPAWNING SEASON.

MALES.				FEMALES.			
Total length in Millimeters.	Tip to first Dorsal Fin.	Tip to Vent.	Vent to Tip of Tail	Total Length in MM.	Tip to first Dorsal Fin.	Tip to Vent.	Vent to Tip of Tail.
365	520	753	247	330	515	760	240
323	518	737	263	310	516	758	242
310	516	735	265	305	541	738	262
345	507	739	261	345	550	768	232
320	506	750	250	335	537	758	242
300	500	733	267	335	537	746	254
328	518	731	269	315	507	761	239
340	514	741	259	305	557	780	220
310	500	725	275	300	533	750	250
275	501	728	272	310	532	758	242
Av. 322	**510**	**737**	**263**	**319**	**532.5**	**757.7**	**242.3**
THE LAKE LAMPREY OUT OF THE SPAWNING SEASON.							
250	540	760	240	350	514	757	243
395	524	747	253	410	512	749	241
405	518	740	260	420	547	750	250
365	548	780	220	281	509	730	270
375	546	746	254	310	500	726	274
378	579	740	260	240	512	730	270
270	500	722	278	285	526	736	264
305	524	737	263	250	520	740	260
370	492	730	270	350	542	743	257
Av. 346	**530**	**744.6**	**255.4**	**321.8**	**520**	**740**	**260**
JUST TRANSFORMED LAKE LAMPREYS.				LARVAL LAMPREYS.			
140	485	714	286	185	502	730	270
141	500	700	300	132	507	719	281
150	500	700	300	125	504	728	272
152	493	700	300	122	524	739	261
155	500	700	300	108	518	740	260
122	491	713	287	112	499	714	286
135	481	703	297	129	488	720	280
127	500	700	300	135	496	718	282
143	517	720	280	135	496	718	282
145	510	717	283	127	504	708	292
Av. 141	**497.7**	**706.7**	**293.3**	**131**	**503.8**	**723.4**	**276.6**

SEA LAMPREYS FROM LAWRENCE, MASS., IN THE SPAWNING SEASON.

MALES.				FEMALES.			
Total length in Millimeters.	Tip to first Dorsal Fin.	Tip to Vent.	Vent to Tip of Tail.	Total Length in MM.	Tip to first Dorsal Fin.	Tip to Vent.	Vent to Tip of Tail.
575	525	747	253	645	527	752	248
670	507	731	269	680	519	735	265
670	507	731	269	755	516	728	272
630	523	738	262	680	514	735	265
700	521	728	272	790	508	734	266
690	514	739	261	660	530	742	258
690	524	731	269	667	539	749	251
740	500	736	264	675	518	733	267
630	523	746	254	715	503	741	259
725	538	744	256	755	529	754	246
Av. 672	**518**	**737**	**263**	**702**	**520**	**740**	**260**
BROOK LAMPREYS IN THE SPAWNING SEASON.							
170	470	718	282	150	533	733	267
167	491	718	282	150	502	720	280
152	513	737	263	160	512	725	275
143	503	706	294	150	513	733	267
148	485	709	291	150	520	733	267
156	512	705	295	145	504	724	276
150	500	720	280	150	500	733	267
167	480	731	269	163	521	724	276
150	486	700	300	155	530	722	278
150	500	701	299	162	512	722	278
Av. 155.3	**494**	**714.5**	**285.5**	**157.5**	**514.7**	**727**	**273**

In each case the specimens were measured without selection, consequently the various sizes are represented as in nature. All the specimens measured had been hardened in Müller's fluid and alcohol, except a few of the lake lampreys out of the spawning season. Part of those were hardened in picric-alcohol and alcohol. Only nine of each sex of the non-spawning ones were in the collection, consequently only nine could be measured. In all the other cases ten were measured. The sexes of the just transformed and the larval lampreys were not separated.

An examination of the table for the lake lampreys in the spawning season will show that the relative proportions of the male and the female shown in the frontispiece of this article

hold good for the lake lampreys generally in the spawning season, and expressed in words the table shows that the differences are as follows: (1), That the average length of the male and the female lake lamprey is approximately the same, being a little greater in the male. (2), The distance of the base of the first dorsal fin from the tip of the head is considerably greater in the female than in the male, or in other words the first dorsal fin is nearer the head and farther from the tail in the male than in the female. (3), In like manner the distance from the tip of the head to the vent is considerably greater in the female than in the male, that is, the abdominal cavity is considerably more extended in the female than the male, and, (4), the tail is consequently shorter. This table shows also, as do the others, the very great individual variation, so that any conclusion which might be drawn from the averages in the table might be invalidated in any individual case. It seems to the writer, therefore that for the determination of species of lampreys, the proportions of fixed parts of the body are not of great value.

Upon comparing the averages in the table for the non-spawning lake lampreys there appears the remarkable fact that, apart from the average greater total length of the male, the proportions are exactly reversed from those obtaining in the spawning season and the dorsal fin in the female is somewhat nearer the head than in the male, the abdomen shorter and the tail longer.*

In order to increase the range of comparison, tables are added of the just transformed lake lamprey, larvæ, and the true sea lamprey.

A glance at the averages for the just transformed lamprey will show that its tail is relatively longer than in the adult, the abdomen shorter, and the first dorsal fin nearer the head. The averages given for the larva are more nearly like those of the non-spawning adult than are those for the just transformed ones.

* The results obtained in this table were so unexpected that all of the specimens were re-examined and remeasured to make sure that the females had not been put inadvertently in the column marked males.

The table for the sea lamprey shows clearly not only average greater length but also in each case the greater length of individuals as compared with the lake lamprey. If one compares the sexes it will be seen that the average female is longer than the average male, thus reversing the conditions obtaining with the lake lamprey. The proportions of the body in the male and the female are more nearly alike than in lake lampreys, but the variations are in the same direction as with the male and female of the lake lamprey.

THE BROOK LAMPREY.

Petromyzon branchialis Linnæus, (1758) *Ammocoetes branchialis.* Cuvier, (1827). Plate IV.

Until the spring of 1886 the brook lamprey was not known in North America outside the Mississippi Valley (Jordan '85). The reason for its non-discovery here before, is due to the fact that so far as is known to the writer, it has never been taken on the fish of the lake, and so far has only been found during the spawning season and immediately after transforming in the autumn. Although the spawning grounds of the brook and the lake lamprey are the same, the time of spawning of the brook lamprey is earlier than that of the lake lamprey the two forms never appearing together. This added to the facts that at the earlier time the water is liable to be high and often turbid, and that the size is small, the numbers comparatively few and the coloration inconspicuous, it will be readily seen why it might escape observation almost any where.

In the spring of 1886, while trying to determine the earliest appearance of the lake lampreys on the spawning ground, three male brook lampreys were found by Prof. S. E. Meek and the writer. They were compared with specimens from the Mississippi Valley and found to agree, and in our preliminary paper at the American Association for the Advancement of Science ('86), one of the points made was "The discovery of *Ammocoetes branchialis*, [the brook lamprey] east of the Mississippi Valley."

By comparing the mouths of the lampreys in plate VI, the character of the dentition will be seen to differ greatly from

that of the lake and of the marine lamprey. This difference in dentition, and perhaps also some other considerations, have led some zoologists to divide the genus Petromyzon into two, *Petromyzon* and *Ammocoetes*, and in this case the brook lamprey is placed in the latter genus.*

In size the brook lamprey varies from 140 to 200 millimeters. The color is nearly uniformly dark in the dorsal half and gradually changes almost to white on the ventral surface. The two dorsal fins are said to be continuous with only a sharp notch between them. As the description of this form in America has been based entirely on specimens taken at the spawning season (Jordan, '85, p. 294), the two dorsals could not be described otherwise than as continuous. But, as with the male lake lamprey, this is a feature of the spawning season. In just transformed ones taken in October, there is a considerable interval between the two dorsals, with only an exceedingly low ridge connecting them, a ridge which in the fresh specimen is very difficult to make out. The figure given is of a preserved specimen (Pl. IV, fig. 13).

The brook lamprey of North America is believed by Jordan to be the same species as the brook lamprey of Europe ('85,

* It seems unfortunate to the writer that, if the genus Petromyzon must be divided, some other name could not have been found for the brook lamprey. When larval lampreys were not known to be the tadpole stage, so to speak of the lampreys, but supposed to be entirely different forms, they were put into an independent genus and called *Ammocoetes*. Upon the discovery, by A. Müller ('56), that the animals previously placed in the genus *Ammocoetes*, were merely a larval stage of a lamprey he made the following suggestion, p. 332: "Somit ist nachgewiesen, dass aus den Neunaugen die Querder entstehen, und dass die Querder zu Neunaugen werden. So sind denn auch die Querder, wo sie sich im Systeme bliken lassen, wegen Führung des falschen Namens anzuhalten, und als Unmündige ihren respectiven Eltern zu unterstellen. Der Name *Ammocoetes* kann fortan nur die Larven der Neunaugen bezeichen, wie *Gyrinus* die der Frösche." Milne-Edwards supports this suggestion and urges that the term be used for the larvae of the Petronyzontidae as the term "tad-pole, gyrinus," is used for the frog's young (Milne-Edwards, '57, tome 2, p. 246). This suggestion has been adopted by nearly all morphologists, and the word is frequently used as an adjective, thus ammocoetes stage, ammocoetes form, etc.

p. 294). Of the European brook lamprey, Seeley ('86, p. 427), says that the dorsal fins may or may not be continuous. He does not give the season when they are continuous and when not so, but it may be inferred that they would be continuous in the spawning season and not in others, as with the American brook lamprey. If the European and North American brook lampreys are really the same species, the distribution is remarkably wide, something as with the marine lamprey; it is also apparently less susceptible to environment than the marine lamprey, for it has apparently been practically unaffected by the special environment of the inland lakes. Certainly also the conditions prevailing in the Mississippi Valley must differ greatly from those found in Europe.

SPAWNING AND THE STRUCTURAL MODIFICATIONS PRECEDING IT.

Structural Modifications.—Besides the change in the gonads (ovary and spermary) there occur marked external and internal changes. Among the most striking of the internal modifications is the gradual change of the liver from the characteristic hepatic color to a bright green. With some examples in which the ova had not yet been shed, there were patches of green intermingled with the ordinary liver color, but in all the green color appears throughout the entire organ before the spawning is completed. This green coloration of the liver appears to be due to the occlusion of the bile ducts and the retention of the katabolic products of the organ. In other than the breeding season, green spherules of liquid of exactly the same color may be found in great abundance in the terminal third of the intestine.

To the unaided eye the change in the liver is simply one of color, but with the alimentary canal the striking change is the diminution in size. From a tube 15 to 20 millimeters in diameter in the lake lamprey, it atrophies to one of 4 or 5 millimeters or even less (Pl. VII, fig. 27, 29, 31–32). The atrophy takes place within two weeks, and begins at the terminal extremity, and extends gradually cephalad until the whole canal

appears like a thread. As no food is taken during the spawning season there is no necessity for digestion, and in the female there is no room for the intestine when the ova are completely matured. This is not the cause of the atrophy, however, for in the male the increase in size of the spermary is less marked than of the ovary in the female, leaving plenty of room for the intestine, still it in many cases is as markedly atrophied as in the other sex.

While the atrophy of the alimentary canal is going on there are certain hypertrophies taking place, differing somewhat in the two sexes, and in the two species. In the male of the lake lamprey there occurs a great increase of the connective tissue along the dorsimeson. This begins about opposite the middle branchiopore and extends to the dorsal fins. This hypertrophy gives rise to a rounded ridge along the back, thus adding a very striking feature to the spawning male (Pl. III, fig. 5, Pl. VII, fig. 31). As an extension of this hypertrophy, the two dorsal fins are approximated to complete fusion in most cases, but apparently no new fin rays are developed. The increase in the connective tissue along the dorsimeson in the female is not marked, except that perhaps the two dorsals appear somewhat approximated. With the female there is a marked hypertrophy in the tissue around the vent thus giving rise to a kind of notch, there is also developed a fin-like fold between the vent and the caudal fin making the caudal fin appear to extend to the vent as in the larvæ of 15 to 20 millimeters in length. In both sexes the urogenital papilla is always present, but in the breeding season it is extended in the male so as to project beyond the level of the body (Pl. III, fig. 6–8).

The abdomen of the female increases markedly in diameter to accommodate the maturing ova ; also as shown by the preceding tables, there seems to be an actual increase in the length of the abdomen, thus shortening the tail. With the male, on the other hand, the abdomen appears to become relatively shorter and the tail longer.

The coloration of the lamprey is very modest out of the breeding season, but in the breeding season there is a great

addition of pigment which appears in the cells of the epidermis, the pigment of the corium remaining about the same. This pigment is yellowish and between the darks spots the color instead of the usual dull gray appears a bright yellow, in some almost golden, thus giving a very striking and handsome appearance. As is common in the lower forms, this coloration is more marked in one sex than in the other, but it is a curious and so far inexplicable fact that some years it is the male that appears in the gorgeous dress while during other years it is the female. For example, during the present year the females of both Cayuga and Seneca lakes were brighter by far than the males, while in 1886 when special note was made of it, it was the males that were more brightly colored.

So far as comparisons are possible the sea lamprey appears to undergo the same changes preparatory to spawning that the lake lamprey does. The specimens personally studied were on their way to the spawning ground and had not reached the same and the changes were not yet completed, but the ridge becomes so prominent during spawning that it has been noticed by fishermen.

With the brook lamprey the changes in the liver are like those occurring in the lake lamprey. The change in the alimentary canal may not be quite so striking as with the lake lamprey. Sufficient material out of the breeding season has not yet been secured to settle that question. In the male the only observed external modifications are the apparent fusion of the dorsal fins, and the considerable elongation of the urogenital papilla. With the female there is the marked anal notch and an apparent anal fin but it is not connected with the caudal fin.

The very striking appearance in the female is due to the swelling in the second dorsal fin thus filling the space between the two. At the first of the season this is merely an œdema, which appears light or semi-translucent, but later, in many cases, it becomes infiltrated with blood and is bright scarlet (Pl. IV, fig. 11–14).

No dorsal ridge is developed in either sex, and apparently the general coloration of the body is unchanged.

Nest Building and Spawning.—As spring approaches the ovary in the mature lampreys increases greatly in size by the addition of food yolk to the multitudinous ova. With the male the actual increase in size of the spermary is not so great, but the ripening sexual products act as a stimulus in both sexes, urging them to complete the cycle of existence by seeking again the clear brooks, far from the lakes, where they themselves began an independent existence several years before. Apparently they start out independently from the various parts of the lake, each one forsaking its prey, and swimming vigorously or stealing a ride by attaching itself to the bottom of some boat moving in the right direction. On they go until the current of the inlet gives them the clue, and they follow it. Frequently also ordinary fishes, bound on the same errand, throng the streams, and then the lampreys, with their inherent desire to be taken care of by the labor of others, fasten to the larger fishes and are carried along up the stream. It not infrequently occurs that from the natural inclination of the stream or from some of man's obstructions, there are rapids or dams to be surmounted. Nothing daunted the lamprey swims up just as far as possible by a tremenduous effort, grasping a stone or other solid so that he should not be carried down stream again, rests for a while and then by a powerful bending and straightening of the serpentine body, a leap is made in the right direction and what is gained is saved by again fastening the mouth to a solid object. This goes on until the obstacle is surmounted if it is not too great. Then without waiting to think of the victory gained the lamprey pushes on up the stream sometimes 8–10 kilometers until clear water and numerous ripples are found. Just above some ripple, the lamprey begins to make ready a secure place for the beginning of a new generation.

From the numerous observations on the brook lampreys it appears that they are somewhat communistic or gregarious, and join in considerable numbers, sometimes 8 to 10, to make a common nest, but with the lake lamprey, while four or five are sometimes in a large nest it more frequently happens that but a single pair is present. If the situation is especially fav-

orable one may see five to ten nests within a small radius; and perhaps the explanation of the very large nests may be that several pairs commenced to build in such close proximity that before they had finished, the nests run together thus producing a single large nest with two or more pairs. Whenever the nest is especially large it has an appearance of a rounded ditch, across the stream not parallel with it.

If one observes the nest building throughout the season it will be seen that those found earliest and those farthest up the stream, contain but one lamprey, and usually the single one is a male. It would thus appear that away down in the very stem form of the vertebrate series the male is the house-builder and takes the lead in preparing for the offspring. The female is not by any means a sluggard, however, and when she joins the male, sets to work with all her might to help complete the nest.

As stated above, the place most commonly selected for a nest is in moderately swift water just above ripples. Now to build the nest the animal has neither hands nor feet, only a mouth, but the mouth is perfectly adapted for grasping by suction and so the lamprey heads up stream, fastens to a stone, the stone being frequently more than twice as heavy as the animal itself. Then with powerful backward or sidewise swimming movements the stone is loosened and dragged down the stream a distance a little greater than the length of the animal, here it is deposited and another grasped and carried down, and so on. If the stone is small it may be carried down by being lifted free from the bottom (Pl. VII, fig. 39). Sometimes a stone will not yield to the most vigorous tugs. In such a case it would be very pleasant to say that two or more joined forces. Two may attach to the same stone if it is large but two have never been seen by the writer to actually join in moving a stone. On the other hand the smaller stones are removed from around the larger one, and from time to time the efforts to remove the large one are renewed until finally it yields to the combined force of the lamprey and the current.

The nests are usually somewhat oval and the diameter parallel with the stream somewhat greater than the length of

the lampreys making them. The central part is usually 15 to 20 centimeters deeper than at the edges so that the whole is nest-like or dish-like in appearance. At the lower edge is always a pile of stones which were carried down in making the nest. As the stones from the upper edge and sides of the nest are loosened the sand is carried down by the stream and lodges in the deepest part of the nest. After the nest has a considerable pile of stones at the lower edge and a good layer of sand in the bottom it is ready to receive the eggs. In ovulation the female secures herself firmly to a large stone at the side or upper edge of the nest so that the body can extend out into the nest, then the male fastens to the female, somewhere near the head, he then winds himself half way around the female, whereupon the two bend their tails downward and stir up the sand by the most vigorous movements. Simultaneously the ova and the milt are forced out in a stream and mingle in the water, and also mingle with the sand. The eggs are coated with an adhesive substance which enables them to adhere to any solid they come in contact with, consequently they stick to the particles of sand that have been stirred up in the water and, as the eggs are themselves heavier than water and made still more so by the particles of sand to which they adhere, they quickly sink to the bottom before the current can carry them below the nest; they are also partly covered by the depositing sand. If many eggs have been extruded, all are not covered and the bottom of the nest may be quite thickly strewn with them. In nearly all cases some remain uncovered. After the pair have "shaken together" as the ovulation is called, they separate and commence at once to remove stones from the upper edge and sides of the nest and pull them down stream as if to enlarge the pile at the lower edge. This was at first puzzling, for the nest is apparently completed before the ovulation begins. The explanation soon became evident, for while immediately after "shaking together" there might be many uncovered eggs, in a very short time they all disappeared, being covered by the sand that was loosened by the removal of the stones and carried down the stream by the current.

The ovulation is repeated at intervals until the eggs are all extruded. If during the spawning the lampreys are disturbed so that one or both leave the nest they soon return. After the spawning is completed, however, they leave it for good and a newly arrived pair may utilize it and thus save themselves much labor. This is proved by catching a pair in a nest and finding the nest occupied by another pair on returning some days later. It is also proved by the fact that from the same nest, during the middle and latter parts of the spawning season, one can obtain eggs apparently but just laid and in the earliest stages of development, and embryos 8 to 10 millimeters in length.

The duration of the spawning season for the brook lamprey is about two weeks. They appear earlier than the lake lampreys and all disappear before the lake lampreys arrive. Frequently the lake lampreys utilize the nests of the brook lampreys as they do the nests of earlier pairs of their own species, as described above The time for the spawning of the brook lamprey usually begins about the 8th of May and lasts till about the 20th. The lake lamprey usually appears about the 25th of May and disappears about the first of July, the height of the spawning time being about the 10th of June. The time varies from year to year and corresponds in general to the advance of the seasons.

As one watches these humble creatures with their pigmy brains and observes with what exactitude they recognize that "to rule nature one must obey her," there comes to one the feeling that the germ, at least, of the highest achievement is present in these our lowly vertebrate allies and that the abyss separating us from them is not so wide after all. If it is urged that all this precision and the resulting efficiency is due to blind instinct then it may be answered that an instinct which guides its possessor to apply the appropriate means to accomplish a desired end, to overcome difficulties not previously encountered by the race and guides it to make the most of favoring circumstances whether they be common ones or those never before utilized, then it must be said that such a guide is a pretty good thing to have after all, and about as valuable

to its possessor as something else, although the something else may have been dignified by the name of reason.

Fate of the Adult Lampreys after Spawning.—As to what becomes of the lampreys after spawning the opinion of authors is conflicting. A. Müller ('56) says concerning it that from the dead ones found at the close of the spawning season and from the fact that in the ovary were eggs of only one size, probably death followed the egg-laying as in case of many insects. Couch ('65), in his work on the fishes of the British Isles remarks concerning this point (Vol. IV, p. 391–392), "As this species of lamprey [the sea lamprey] enters rivers for the purpose of spawning in the spring, this is the season of highest perfection ; but immediately after the shedding of the roe so great a change takes place, that they are not only weakened and emaciated, but it has been believed that death is commonly the result. But this last supposition at least is not correct. . . . . Soon after spawning the parent fish returns to the sea." Seeley ('86), says concerning the sea lamprey, "After spawning the fish is exhausted and goes down to the sea." Of the river lamprey he says, "After spawning the lampern usually dies ; " and of the brook lamprey, "After spawning the old fishes probably die." Benecke, ('80–81), as quoted by Goode ('84), remarks upon this point, "After the eggs have been deposited, the lampreys die." The proof in each case is not proof, but probability, from each author's standpoint, the strongest argument being that of A. Müller,—that the ova in the ovaries are all of the same size.

Unfortunately the fate of the lampreys after spawning has not been determined by the writer, although special pains were taken to determine it. Several facts seemed to indicate that, with both species, most of them return to the lake after spawning, for in the middle and later part of the season many lampreys are found going down the stream or attached to stones below the nesting places. On examination such lampreys were always with empty gonads. As to their death on the spawning grounds, especial care was taken to look for the dead, but in all the years of investigation not more than 10 dead ones were seen. This does not indicate the number that

might have actually died, however, for birds of prey hovering over the water would be very liable to catch any that were *in extremis*. Nature has so many ways to dispose of dead bodies that the number seen even on careful investigation is small, even though the actual mortality may be great.

In the last part of the season many were affected by saprolegnia, especially where the epithelium had been injured by the attachment of another lamprey. An additional argument in favor of the death of the lampreys after spawning, is the condition of the alimentary canal and the liver. There would need to be almost a new building of the alimentary canal. And then enforcing the argument from the absence of small ova in the ovary after spawning it is to be said that even in the larva the eggs are of considerable size (Pl. VII, fig. 38), so that if the lampreys that had spawned were to return to the lake and re-acquire ova a greater development in the ovary would be required than takes place between late larval life and sexual maturity ; a development requiring from two and one-half to three and one-half years in the lake lamprey.

An effort was made to determine the matter experimentally by transferring lampreys that had spawned to water containing cat-fish (*Amiurus nebulosus*), as the lampreys seem particularly fond of cat-fish. The conditions were very unnatural as the only available place was a cold spring. The cat-fish soon died and the lampreys also, without attempting to feed on the live or dead fish. It seems to the writer that the experimental method is the only one promising satisfactorily to settle this vexed question, a question important alike from the scientific and from the economic stand-points. If a pond through which the water from the stream in which they spawn or one connected with the lake were stocked with cat-fish or suckers (*Amiurus* or *Catostomus*), fishes which are frequently attacked by lampreys, and then if lampreys were placed there after spawning one could determine the duration of life after spawning under natural conditions of water and plentiful food. There is no difficulty whatsoever in keeping lampreys alive and in good condition out of the spawning season even in a large aquarium where there are other fishes. Indeed the lam-

preys are so vigorous and aggressive that, when hungry, they will attack the ganoid fish, *Amia calva*, and rasp away the scales sufficiently to extract blood from the amia. If they naturally return to the lake and resume their ordinary mode of life there should not be the slightest difficulty in determining it under the natural conditions just mentioned. It is hoped that suitable facilities may be afforded at some future time to settle definitely this important question and also several others that have arisen in the study of the various stages in the life history of these animals.

DEVELOPMENT OF THE OVUM AND LARVAL LIFE.

The ripe ova are about one millimeter in diameter and nearly spherical. They are very opaque from the abundance of opaque food yolk, and each is surrounded by a thin layer of material which is very adhesive upon exposure to either air or water, consequently the eggs adhere to whatever solid body they come in contact. The adhesion is not very permanent, however, as after a day or two they are easily detached.

Some eggs of the brook lamprey were fertilized and kept until the larvæ were hatched. The segmentation is total and unequal as in the amphibia, and the development proceeds with great rapidity ; after eleven days the heart beats are plainly visible. In 14 days the mouth is shark-like and on the ventral side, and the blood vessels extend around the gill slits. In 18 days the eyes are clearly shown, respiration and the movements of the velum are evident and the mouth has assumed the larval appearance with the hooded dorsal lip so characteristic of the older larvæ. The fins are represented by a continuous fold from a point about opposite the 4th branchiopore along the dorsimeson and around the tail on the ventrimeson to the vent. In swimming the larva goes with a wriggling motion ; it holds itself dorsal side up as do the older larvæ when swimming and like the older ones rests on the side when quiet.

As was shown by Calberla ('77), the nervous system develops as a solid cord and becomes a hollow tube only later in the course of development. In this respect the lamprey

agrees with the teleosts and the ganoids, so far as they have been investigated (Calberla, '77, Balfour, '81). Other references to the embryology of the lamprey will be found in the bibliography at the end.

In nature the young larvæ live in the sand in the bottom of the nest where the eggs were deposited by the parents. Sometimes the larger ones are found most abundantly in the sand and gravel under the pile of stones bordering the lower edge of the nest. This may have given rise to the prevalent notion that the pile of stones is the real nest. One can obtain the embryos very easily by shoveling up the sand from the bottom of a nest. If water is then added to wash away the mud, and the sand is shaken lightly, the eggs or embryos or both appear on the surface, and are readily detected by the light color of the eggs or the greenish color of the food yolk in the embryo of 8 to 10 millimeters. After the larvæ are 10 to 15 millimeters in length it is far more difficult to secure them as they are less conspicuous and far more active. Then too, they exhibit already the habits of older larvæ and very quickly disappear in the sand.

The exact time the larvæ remain in the nest and the stage of development reached by them before leaving it is not known with exactitude. Already on July 31st, larvæ 30 mm. long were found while searching for large larvæ. A few days later a thorough exploration was made by my assistant, G. S. Hopkins, D.Sc. both in the nests and in the sand banks at the concavity of the stream where the larger larvæ are found throughout the year (Pl. VII, fig. 40). None could be found in the nests at the bottom of the stream, but in the sand at the side of the stream many of all sizes were obtained, some of them being only 16 millimeters in length. Consequently it is believed that the larvæ remain in the nests only about one month or until they attain a length of 12 to 15 millimeters. Whether they voluntarily leave the nest or whether the rapid current of some sudden rise in the stream, as after a heavy storm, washes them out of the nest is not known. It is believed, however, that they leave the nest voluntarily, for, on account of the conformation of the nest, any moderate in-

crease in the stream would tend to cover the larvæ still deeper.

Larval Life.—After the larvæ leave the nest they wander down the stream until some suitable place composed of sand and mud is found. This suitable place is most often in the concavity of the stream where the water flows slowly and there is not great danger of being washed away by every freshet. Judging from specimens in the laboratory that were placed in glass vessels with water, and sand from the native habitat, each larva has a canal or burrow of its own. This burrow usually opens on the surface of the sand. In this burrow the larva remains, changing its position at will and also making a new burrow with a new surface opening as inclination or necessity demands. In those observed in a glass vessel where there could be no doubt, the canal was curved, the convexity of the curve being downward (Pl. VIII, fig. 49). The larva was curved correspondingly ; but the dorsal side was always up as shown in the drawing. Often in moving to and fro in the canal the tail would be higher than the head. If disturbed the larva leaves the burrow and worms itself through the sand with great alacrity. They do not leave the protection of the sand if they can possibly avoid it. In their natural home beside the streams, they are usually only a few centimeters under the surface of the sand and frequently not more than 15 to 40 centimeters below the water level. In taking them the sand is shoveled up from the stream and carried out to the shore and placed on the bank or upon something else so that the water may drain away. As soon as the sand is pretty well drained, any larvæ present wriggle out to the surface where they can be seen. To obtain the smaller ones it is necessary to take somewhat more care and spread the sand out in a thin layer ; sometimes also it is advantageous to pour water over it.

The way in which the larvæ enter the sand from the water and the way they move around in the sand was very easily and satisfactorily demonstrated by placing some of the sand from the native habitat in a glass dish and partly filling it with water. The sand was washed to avoid turbidity then a

larva introduced. If the creature is vigorous it almost immediately commences to bury itself, and in the following manner: It stands almost vertically on its head and then makes most vigorous swimming movements. At the same time the head with its hood-like dorsal lip is twisted from side to side something as one turns the hand in trying to force an awl into wood or leather. In a short time the animal will bury itself to about the extent of its branchial apparatus, that is until the sand affords a kind of hold for it. The animal then ceases to go directly downward, but with a serpentine movement, constantly twisting the head from side to side to open the sand, it goes more nearly horizontally till the body is entirely covered. Once in the sand the creature moves around with great ease, the head and hood-like dorsal lip serving by their stiffness and mobility to part the sand. It soon makes a burrow and the opening to the surface of the sand. In this burrow it can move to and fro at will. The sand seems to be packed in some way so that it does not cave in and fill the canal.

In discussing the habits of the larvæ it is frequently stated that they have a great dislike to light and swim around in the vessel in which they are placed until exhausted and they die. From my own experiments the larvæ do not seem to have a great dislike to light, but rather there is a sense of insecurity when not covered by the sand. Experiments were carried on for weeks with those in glass vessels to see if, when the burrows were next the glass, and that side turned to the light the larvæ would move away from the light, as they could very easily do if desired. Sometimes they would make a new burrow on the side from the light, but nearly as often the change would be made from the shaded to the light side. It thus appeared that if the animals were protected by being in a normal habitat in the sand the restlessness mentioned by authors as due to light would not be observed. Furthermore one was kept alive in a small globe, hanging, glass aquarium with other aquatic animals from Christmas till the following May. In it there was no sand present and the animal was thus constantly exposed to the light throughout the day.

Whenever a larva swims it is always dorsal side up, but in resting on the top of the sand or on the bottom of a vessel of water it lies on the side. Apparently the side on which it rests is a matter of chance as it is sometimes the left and sometimes the right.

Comparison of the Larva with the Adult.—As one watches the development of a lamprey's ovum it is seen that in a very short time, 10 to 15 days, the embryo assumes characters markedly like its parent; but a closer study will show very marked differences. Instead of a circular, sucking mouth armed with teeth, the mouth is hooded and the entrance guarded by a very perfect sieve (Pl. VI, fig. 22), and between the mouth and gills will be seen a reddish body that moves to and fro rhythmically and in unison with the movements of the branchial apparatus.

If the branchial chamber is explored the seven branchial openings on each side will not be found to open, each into a separate sac or pouch, but into a large common chamber, a chamber serving also for an œsophagus. The eyes, too although visible do not reach the surface, but remain quite deeply imbedded. Many other structural differences occur, but a sufficient number have been named. In habits the difference is as striking as the difference of structure; the parent is a free-booter, the offspring lives an orderly and isolated life. It is no wonder that naturalists and fishermen should have agreed that they were different animals; that they were different stages of the same animal probably did not enter their minds.

So strikingly unlike are frogs and their young, the tadpoles, that it would be deemed almost incredible that one is the offspring and would assume the appearance of its parent if the facts were not forced upon every one that is at all observant. The transformations in insect life, too, are even more marvelous, but from their frequency are taken as matters of course. Apparently, a fisherman and naturalist of Strassburg Leonhart Boldner in 1666, knew of the metamorphosis of the lampreys, and that the larvæ were larvæ and not distinct animals. But this was lost sight of, and the knowledge

of the scientific world dates from the discoveries and the publication of A. Müller, 1856. (See note on p. 437 above).

Duration of the Larval Period.—The time required for the larva to prepare itself for adult life is not known. It has been estimated at three to four years. The reasons for assigning that time are: The larvæ that may be obtained from the natural habitat at any season of the year are of such varying sizes that it is believed that from three to four generations are represented. The first of September for example, one may obtain from the same bank or bed, as the fishermen call it, lampreys in various stages of transformation, larvæ about two-thirds as large as the transforming ones and so on down to the generation of that year, which are from 15 to 40 millimeters in length. This like the supposed death of the adults after spawning is one of the questions that must be determined experimentally. As the larvæ are easily kept for six months to a year in an aquarium with sand, it would doubtless be very easy to keep them from the egg until transformation, by imitating closely the conditions obtaining in their native home.

Transformation and Duration of Adult Life.—When the larvæ attain a length of 120 to 160 millimeters for the lake lamprey or sometimes as great a length as 200 millimeters for the brook lamprey, they transform to the adult condition. The brook lamprey does not apparently increase in length after transformation, for many of the transformed ones at the spawning season are of less size than the just transformed ones. There is, however, some increase in the bulk of the body, and a considerable increase in the gonads. As shown in plate vii, figures 35 and 36, the ova and the sperm mother-cells are in about the same stage of development as the lake lamprey six months before spawning. It is believed from this that the brook lamprey attains nearly its full growth before transforming, and that the free life in the water is only about six months, that is from the transformation in the autumn, August and September and perhaps October, till the following May.

The lake lamprey upon transforming is only about ½ to

$\frac{1}{4}$th the length and probably not one $\frac{1}{10}$th bulk of the spawning ones. The gonads are small and the ovary and ova are minute but perfectly recognizable on transforming. The comparative size is given on plate vii. The gonad of the male is very small indeed, and the sperm mother-cells not far advanced. To attain the size and maturity of the spawning ones it is believed that two or three years are required. This conclusion is reached by the size and development of individuals caught in various months of the year. For example, while the lake lamprey is spawning, specimens have been taken from the lake with the intestine large and full of blood and with ova of about half or one-third the size of the mature ones. In others of about 200 or 225 millimeters length the ova are still smaller. The smallest ones are supposed to have transformed six to eight months previously and those next in size a year and a half earlier. The absolute bulk of fishes depends so largely upon the food supply that size of body alone is not a good test of maturity. The size and stage of development of the sexual organs is a safer guide. Following this guide it seems very probable that it requires either one year and a half, two years and a half, or three years and a half for the small, just transformed larva of 150 millimeters to attain a length of 450 millimeters, or rather that ova of the size shown in plate vii, figure 34 A, require that time to reach the size and maturity of the egg shown in 32 A. This question like those previously mentioned can be definitely settled only by rather expensive experimentation. That it has an important scientific interest all biologists will agree; that it also has a very important economic bearing may be seen also when one reflects how many food fishes are either destroyed or greatly weakened by the parasitic adult lampreys.

The transformation of the larva into the adult is usually described as taking place in a few days. In three or four (en trois ou quatre jours) according to Bujor ('91), for the European brook lamprey (P. planeri, or P. branchialis). The time given by Müller is longer, 10 to 26 days. My own observations accord more with those of Müller. The first external signs of transformation is the appearance of the eyes upon the

surface and the development of the sensory papillae in the characteristic curved line interrupted by the eye (Pl. VIII, fig. 50). Looked at in a strong light the eyes appear in a dorsal view like clear spaces; looked at from the side the black pigment, especially in the dorsal half, is very evident. The mouth in this stage is precisely the same as the larva to all appearance and so is the general coloration of the body. In a somewhat later stage the eyes are still more evident, but appear dull and as if covered by only a semitranslucent membrane. The mouth has no longer the wide open appearance of the larva but has become greatly contracted; the dorsal and ventral lips are becoming fused and the oral tentacles arrange themselves as shown in figure 23. The appearance is exactly as if the papillæ or tentacles were to form the basis or foundation for the future teeth. Several days (20) later the eyes are less turbid and the oral tentacles have lost their branched ends and have become blunt papillæ. In one kept in a large glass vessel with sand and stones, changing the water frequently, the changes just described were gone through in 25 days. But it is believed that nearly as many more days are needed to develop the large, clear eyes of the adult form and the enlarged sucking disc with horny teeth; so that with those investigated by me the metamorphosis cannot be said to go on very rapidly, but rather, very slowly. One of the striking external changes also is the gradual darkening from a brownish gray to a blue black, which is so rich and soft that it appears like velvet. The pineal eye then appears like a snow white, rounded spot. Later it is partly overshadowed by the thickening epithelium and looks dull (Pl. VIII, fig. 50). A striking change in attitude also occurs. The animal rests dorsal side up and not on the left or the right side as with the larva.

Corresponding with the external changes, there are profound internal changes. The intestine no longer opens into the bronchus, but a new œsophagus is developed along the dorsal wall of the bronchus and finally opens cephalad of it very near the mouth. The gills cease to be in a common chamber and are divided, each one forming a pouch which opens to the exterior by the branchiopore as in the larva and into the

common bronchus by a small opening about the size of the external opening. The velum gradually atrophies and soon almost disappears. It is stated by Bujor that in the metamorphosis, the tissues return to an embryonic condition and then are reformed into the tissues of the adult. "Les différents tissus des organes larvaires se régénèrent complètement pendant la métamorphose," (Bujor, '91, pp. 77, 88). Especial care was taken in investigating the transformation to determine something of the activity of the animals and their mode of life. The first transforming ones were obtained the last of August. The last just transformed ones from the native habitat were obtained the middle of October. Aquaria were prepared with sand and gravel, thus imitating as closely as possible the natural conditions. Into these aquaria the transforming animals were placed as they were received and each aquarium carefully labeled with the date and the stage of development. All of the animals that were in good condition very soon disappeared in the sand. Those with a fully developed sucking mouth surrounded by the oral fringe of papillæ (Pl. VII, fig. 19–21), also buried themselves. Some of these were so far advanced that the horny tips to the teeth were already visible with a lens. It is therefore believed that the animals, in nature, remain under the protection of their early home until they are fully armed and ready to get their food in the usual adult fashion.

The activity of the animals seemed not at all lessened. In a vessel of water they swam with the same vigor as untransforming larvæ and frequently like them made vertical leaps of 10 to 20 centimeters to escape from the dish. The respiration seemed in no way interfered with. So far as certain structures are concerned, at least, there seemed no tendency to return to an embryonic condition. The ova, for example, in 100 millimeter larvæ have the unmistakable characters of the ova in young adults. None of these characters are lost during transformation. Certain profound changes take place, that is certain, but these changes appear to the writer rather the additions to or rearrangement of tissues common alike to the larva and the adult, new structures also appear and purely

larval organs like the velum atrophy. So far as the liver and its duct are concerned it is almost universally stated that in the European brook lamprey the bile duct loses its connection with the intestine upon transformation. This is not the condition in the lake lamprey and in many examples, at least of the sea lamprey. It is only upon the atrophy of the intestine at the breeding season that the bile duct is occluded. Then the liver assumes an emerald green color as stated above (p. 438). From the numerous observations made by the writer on transforming lake lampreys and sea lampreys from the Susquehanna River, there is not a period of quiescence comparable to the pupa stage of insects; such a period would be expected with so great a histolysis and subsequent histogenesis as described by Bujor ('91) for the European form of the brook lamprey.

In collecting the transforming lampreys the same method is employed as described above for the untransforming larvæ. It is well, however, to have a dip net with a long handle, for the transforming ones more readily leave the sand when it is disturbed by the shovel, and attempt to swim away in the stream. With the dip net these may frequently be caught.

Up to the present time there has been no way discovered of distinguishing the larvæ of the lake and of the brook lamprey. As the two species occupy the same spawning ground and sometimes spawn in the same nest great care is necessary in order not to confuse the two. After the larvæ leave the nest they apparently go to the same sand bed. There are certain peculiarities about the one figured in plate iv that might lead one to diagnose it as the larva of a brook lamprey. Here again, only a carefully conducted experiment would give definite and reliable information.

If one can keep the transforming ones alive until the dental papillæ appear on the oral disc the distinction is as clearly marked in the two species as in the adult, for there is the same definiteness of arrangement, and the same arrangement of dental papillæ in the young as in the horny teeth of the adult. The general appearance of the brook and the lake lamprey is also as strikingly unlike at this stage as in any subsequent one.

ECONOMICS.

From the human stand-point, beneficial or injurious, as applied to an animal or plant relates solely to the supposed advantage or disadvantage to the human race that it subserves. No doubt from the economical stand-point of the animal or plant, judge and prisoner would change places. In this economical consideration two questions arise: First, in what way does this animal or plant subserve man in supplying food or clothing and secondly, does it destroy, for its own use, food or clothing that might otherwise be utilized by man.

To answer these two simple questions it is only necessary to find out the food of an animal, and also the animals for which it in turn serves as food.

Food and Uses of the Larva.—The food of the larva consists of microscopic organisms separated in some way from the constant stream of water drawn into the combined œsophageal and branchial chamber. It thus appears that in its larval life the lamprey is not injurious to man by destroying food that he wishes, directly or indirectly, to utilize for his own benefit. On the other hand, from the tenacity with which the larvæ retain life they have been found excellent bait for all kinds of ordinary carnivorous fishes. The fishermen along the Cayuga and Seneca Lake inlets make considerable use of the larvæ for bait; this form of bait has not up to the present been much used in the lake fisheries, as apparently its excellence is unknown. At Owego, on the Susquehanna River, however, quite a business is carried on in supplying larval lampreys to fishermen of all kinds, and many are shipped to distant points.

As no distinction is yet known between the larvæ of the brook and of the lake or sea lamprey, all larvæ may be classed as non-injurious and as positively beneficial by serving for bait, and thus in aiding man to obtain food fishes.

Economics of the Adults.—Unlike the larva the adult lamprey is largely or wholly parasitic, and in obtaining its food destroys or injures the fishes used by man as food. It is stated by Günther ('53, p. 133), that the food of the lamprey (*P. marinus* and *P. fluviatilis*) consists of worms and insects,

and fishes to which it attaches itself. He is followed by nearly all authors, more especially in describing the food of the brook and river lampreys. From personal observations, the food of the brook lamprey of the lake region has not been determined, as none have been taken out of the breeding season except those which were transforming. From their small size (150–200 millimeters) and the probable shortness of adult life, the injury to the larger food fishes in any case must be considered slight. This is especially true of the region under consideration, for in addition to the smallness in size and probable shortness of life, they are few in number. While it is not at all difficult to get 200 to 400 lake lampreys from the Cayuga Lake inlet during one spawning season, one must work quite persistently to obtain 75 to 100 brook lampreys.

With reference to the usefulness of the brook lamprey in New York, it may be put down as nil. In England, according to Couch ('65) and Seeley ('86), the adult river lamprey which is very closely allied to the brook lamprey, or specifically identical with it (Schneider, '79, Shipley '87), was formerly much used in the cod and turbot and other deep sea fisheries. It is stated by Seeley that the lamprey fishery begins in August and continues till March, and that in that time as many as 450,000 have been taken and used as bait in one year.

With reference to the lake lamprey, the conditions are quite different from those described for the brook lamprey. In the first place the lake lamprey exists in large numbers, and lives a parasitic life from one and a half to three and a half years. Of all the specimens obtained out of the breeding season, either the digesting part of the alimentary canal was empty or it contained blood. No partly digested worms or insects or small fish or fish flesh were ever found, although diligent search was made; consequently it is believed that the lake lamprey is wholly parasitic during its adult life and lives on the blood sucked from other fishes. From the structure of the mouth and the opening to the œsophagus in the adult, one might also infer that liquid food was used and that this was obtained by suction as with a leech.

From observations on the lampreys in flat sided, glass jars, and by experiments in allowing them to fasten to the hand, the process of attachment appears to be as follows: The oral disc is quite widely expanded and pressed suddenly against whatever the lamprey wishes to fasten to. Almost instantly the mouth is somewhat arched and any water that may be present drawn into the bronchus. The circum-oral fringe of papillæ with the continuous fold of mucosa bordering the fringe, serves to fill any irregularities and make the contact, air and water tight, so that upon lessening the pressure within the mouth the adhesion becomes very perfect. So perfect is it, that such a hard scaled and vigorous fish as the ganoid, *Amia calva*, can rarely prevent the attachment and adhesion although the most violent efforts are made. If they are attached to stones of moderate size, the stone is frequently brought out with the lamprey if the animal is jerked up suddenly. In letting go its hold all that is necessary for the lamprey is to fill the disc with water from the respiratory bronchus, whereupon suction ceases and the animal is free. In feeding, the sharp teeth pressed against the skin of the animal to which it is attached, naturally calls the blood to the place. This hyperæmia is caused even more by the suction. At the same time the piston-like tongue with its powerful muscles and the saw-like teeth soon rasps a hole through the skin. The blood is then sucked from the fish and swallowed. The whole operation is something like the extraction of blood by a leech. The lamprey may remain upon a fish so long as it supplies sufficient nutriment. Sometimes the fish becomes exceedingly pale and weak so that it floats near the surface. In such a case, the fishermen know immediately that there is a lamprey attached to the fish, and, with a dip net, usually have no great trouble in catching both. The birds of prey also make this their opportunity and frequently carry off the floating fish, the lamprey sometimes remaining attached until it has been carried a considerable distance into the air.

According to one intelligent fisherman, who has spent nearly fifty years by the lake, some of the fishes, when a lamprey attacks them, will rise to the surface and turn over on the

side so that the lamprey's head and branchial apparatus are out of water. By this means the lamprey is partly suffocated and lets go its hold, thus freeing the fish.

That the injury to the food fishes is very great may be inferred from the fact that sometimes out of 15 cat fish caught on a set line in one night, 10–12 have great raw sores where a lamprey has attacked them. In the spring, too, when the suckers (*Catostomus*) run up to spawn, very many of them carry a lamprey, and naturally by the great drain of blood that it causes, the fish must be weakened, so that obstacles on the way to the spawning ground are less liable to be surmounted than as if the fish were in full vigor.

As stated above, during a single season over a thousand lampreys were caught in the Cayuga Lake inlet. If these had spent from two to three years infesting the fishes of the lake they probably did more to reduce the number of available food fishes than the fishermen.

In 1891, on account of the lack of rain and the clearness of the water in the streams at the spawning time, conditions were very favorable for determining the number of nests in the Cayuga Lake inlet. This was done for about 10 kilometers, and 400 nests found. If each nest had been inhabited by a single pair, then 800 lampreys visited the inlet for spawing during that spring; but in 1886 over 1000 were known to have been caught from the inlet, and furthermore by direct observation some of the nests are utilized by at least two pairs of lampreys, so that probably the 400 nests represented a visit of 1000 to 1200 lampreys and perhaps more. The males are usually somewhat in excess so that probably there were from four to six hundred females. The number of eggs in the ovary of a lamprey of moderate size was estimated in the usual way by weighing a small piece and counting the eggs in it and then weighing the whole ovary. The eggs present in the whole ovary is then estimated by a simple proportion. In the case mentioned, the ovary was found to contain 65,000 ova. (A sea lamprey from the Merrimac River was found, by the same method, to contain 236,000 ova). If each of the females that were on the spawning

grounds that year deposited 65,000 ova there would have been laid 65000×400=26,000,000. Many of the ova fail of fertilization and many also fail to develop even if fertilized so that of the possible twenty-six million young lampreys from the spawn of a season, possibly not over 4 or 5 thousand reach the sand beds; and from the further decimation of these the numbers in the lake remain approximately uniform as with other animals in nature.

Ridding the Lakes of Lampreys.—From the foregoing account of the life history of the lamprey it will be seen that it has a single very weak point, viz., leaving the lake and running up the tributaries to spawn. This seems to be the only weak point at which the lamprey can be attacked with a hope of exterminating it. This point is rendered still weaker from the fact that in Cayuga Lake, and in Seneca Lake, so far as explored, the lampreys run up the inlet at the head of the lake only, and do not spawn in the tributaries entering the lake at intervals on each side. Some of the lateral tributaries seem well adapted for the lamprey's spawning grounds; these streams are used by other fishes, but the most careful exploration under favorable circumstances gave no sign of the lampreys. Also, as will be seen by examining the map (Pl. II), the large creek (Fall Creek) entering the head of Cayuga Lake by a separate entrance, has never been known to contain lampreys. Careful personal search was made for several seasons and inquiry made of those familiar with the creek, but none were ever found or heard of. This may be due to the nearness of the falls in the course of the stream. The creeks joining the inlet (Cascadilla and Six Mile creeks) contain them. Formerly they were very abundant in both, but the water is not now so plentiful and then both extend for a considerable distance through the city. At present it is the main stream that is most frequented and employed by the lampreys for spawning. The lampreys must be destroyed before spawning if they are to be exterminated. Nothing would be easier than to do this. A dam with a fish-way, the fish-way leading into an isolated enclosure where the lampreys could be easily removed and disposed of, or a weir

of some kind could be constructed at slight expense. If this could be continued for three to four years in all the lakes and in the Oswego River, the race could be extinguished and the lake wholly freed from their devastations. So vulnerable is this point in the lampreys defenses, that even in great rivers, where dams exist, the fish-ways could be utilized to free the river of lampreys as well as to allow the more valuable food fishes to run up and spawn. To be sure, in the Merrimac and Connecticut rivers the lampreys have been largely utilized for food, but if one considers the damage these monstrous parasites must do to the ocean fishes it will be seen that too dear a price is paid for the food they furnish. It seems to the writer that from every economical standpoint it would be advantageous to rid the world entirely of the lampreys. It would certainly be greatly to the advantage of the fisheries of the State of New York if all were destroyed. Naturally, however, the student of biology must mourn the loss of a form so interesting and so instructive.

RESPIRATION AND THE RESPIRATORY MECHANISM IN THE LARVA AND IN THE ADULT.

In the lampreys, the respiration is wholly aquatic. They do not come to the surface and take in air as do many fishes. As the dissolved oxygen is only 6 cubic centimeters in 1,000 c. c. of water, while in the air there are 209 c.c. of oxygen in 1,000 c.c. of air, it follows that an animal like the lamprey with a purely aquatic respiration must either be very sluggish, or a very perfect respiratory *mechanism* must be present in order that it may obtain the needed oxygen from the meager supply in the water. In the lamprey there is a very perfect respiratory mechanism. If one considers also the ease and completeness with which the carbon dioxid is eliminated in aquatic respiration, and the fact that with the lamprey, from its habits, only occasionally are great exertion and rapid movement necessary, as in searching for prey and in spawning, with the attendant nest building, it will be seen that the lamprey is very well off for an animal with aquatic respira-

tion. It may be further stated that when the lamprey has gorged itself with blood, the first marked change appearing in the blood taken as food is the reduction of the oxy-hemoglobin to hemoglobin. Without doubt the oxygen stored in the hemoglobin by the respiratory activity of its prey is used for respiratory purposes by the lamprey. As pointed out by Bert ('70) and others, any thin and highly vascular membrane may serve as a respiratory membrane. The alimentary canal of the lamprey answers admirably these conditions, and on opening the gorged intestine of a lamprey just taken from a fish, one can trace with the eye alone the gradual transformation of the oxygenated blood through gradually darkening shades until the blood is almost black. Examined with the micro-spectroscope, the transformation can be followed with great definiteness and by agitating the black blood with air it reddens and the two characteristic bands of oxy-hemoglobin reappear. No doubt this use of the oxygen obtained by another fish is of considerable importance to the lamprey, and there is realized by it very perfectly the obtaining of ordinary and gaseous food at the same time.

With the larva, the motions are very energetic for a short time, then the animal lies on its side panting, as it were, the respirations are so rapid. In nature, however, only very rarely is great exertion necessary, as in burying itself in sand after voluntarily or accidentally becoming free in the water, also by moving through the sand for a more favorable locality. Almost the only other muscular activity consists, not in moving the whole body, but in pumping water into and out of the broncho-œsophageal chamber for the combined purpose of respiration and obtaining food.

Respiratory Mechanism and Movements in the Larva.—If a larval lamprey is placed in a glass vessel with coarse sand and a plentiful supply of water it will very soon make a suitable burrow or canal in which to live. Very frequently the burrow will be made in part next to the glass, in which case one may observe with great definiteness all the respiratory movements, especially if a magnifier is used. It is seen that in repose the respirations are not far from 100 per minute, sometimes

less, often many more. If the head is exposed and there are any particles in the water a constant stream is seen to flow into the mouth. Only when the respirations are very slow is the stream into the mouth intermittent.

As the burrow is ordinarily open, as shown in Pl. VIII, Fig. 49, some particles of corn starch dropped into it diffuse in the water and one can then see the direction of the stream from the particles of starch. Starch is the most satisfactory substance used with the larval lampreys as they are not irritated by it. In fact it is taken into the alimentary canal. In case the water contains minute filaments these will often be drawn by the stream to the mouth, but the sieve or net work formed by the oral tentacles catches them and prevents their entrance into the respiratory chamber. Whenever the oral sieve becomes at all clogged by adhering particles, the current is reversed and the offending débris washed off most energetically. If attention is directed to the branchiopores or gill openings, it is seen that, with every constriction, streams of water shoot out obliquely caudad. The valves over the branchiopores (Pl. VIII, Fig. 52, *vl.*) project outward, but as soon as the branchial apparatus expands for inspiration the valve closes the branchiopore so that water does not enter it, and thus all the water entering the gill cavities must enter through the mouth. It is seen also that while the stream into the mouth is practically continuous, its exit through the branchiopores is intermittent.

If a larva is placed in a dish of water it swims around somewhat aimlessly but rapidly for a time, but finally rests on its side. The side on which it lies seems to be a matter of indifference, and is therefore sometimes the right and sometimes the left. If the water in the vessel is not too deep, the current made by the jets of water from the branchiopores is easily demonstrated by putting bits of wood or cork on the water over the gill-openings. They follow the current almost directly caudad along the whole length of the larva. If the position of the larva is noted, and then it is observed again after 15 or 20 minutes it is seen that it has moved cephalad or forward due to the recoil or reaction of the jets of water forced

from the gills. The forward movement is not so great, however, as might be expected from the strength of the backward current, and the slight retardation due to the friction of the bottom of the vessel. While the animal is lying on its side, the current into the mouth is clearly seen by dropping a little starch into the water. The currents can also be very satisfactorily studied by placing the animal in a test-tube or narrow jar with water and a little corn starch.

Whenever the head of the larval lamprey can be seen in a good light, an arched, reddish, moving body is visible through the translucent body wall between the opening of the mouth and first gill. This is in rhythmical motion toward and away from the mouth. It is the *velum*, composed of two symmetrically placed, arched curtains which perform the double function of valve to prevent the water from going out through the mouth when the branchial apparatus is constricted, and also of moving by its own musculature something as the diaphragm of a mammal and thus alternately increasing and diminishing the size of the branchial cavity. If the movement is carefully watched and compared with the alternate constriction and expansion of the branchial apparatus, it is seen that the expansion of the branchial apparatus and the cephalic or forward movement of the velum coincide, both thus acting to increase the size of the branchial chamber and therefore to draw water into the branchial cavity, that is, both are inspirators. On the other hand, in expiration the velum is drawn caudad at the same time that the branchial chamber is constricted and thus a double diminution of the capacity of the branchial chamber results and the expiration is complete. This caudal movement of the velum has also tended to draw water into the space between the velum and the sieve like tentacles. This water is drawn into the branchial chamber immediately upon the expansion of the branchial chamber and the forward movement of the velum. Owing to the valves over the branchiopores, the branchial chamber can only be filled through the mouth, and a current is drawn into the mouth both in expiration by the caudally moving velum, and in inspiration by the expanding branchial chamber, hence it

follows that the current going in at the mouth must be constant, unless the respiratory movements are exceedingly slow. The reason why the cephalically moving velum does not force the water out of the mouth in narrowing the space between the sieve and the velum is that, as the velum moves forward, it leaves an equal space behind it and thus aspiration is produced in the branchial chamber, and as there is nothing to support the thin mesal edges of the velar folds, they move laterally and thus make a free passage for the water to the branchial chamber, so that the action of the velum alone tends constantly to aspirate the water into the mouth. When the velum is aided by the expanding branchial chamber in inspiration, an increased aspiration is insured and so much the more is there a constant inflowing current.

By careful experiment on transforming larvæ it was found that they continued to take a constant current into the mouth even after they were able to attach themselves to the sides of the vessel containing them by the almost completely developed sucking disc. Those experimented upon buried themselves in the sand and gravel whenever they were given opportunity; it is believed therefore, that until the young lamprey is entirely transformed and swims freely in the water or becomes attached to a fish, water is inspired through the mouth as well as through the branchiopores, but, in expiration, it passes out only through the branchiopores, except when the branchial apparatus is being cleared of particles taken in with the respiratory currents. The action of the velum may be most perfectly shown by thoroughly etherizing a larva and then carefully removing the ventral body wall between the velum and tentacles so that the velum may be very clearly seen. If now the animal is set up endwise in water one can study very satisfactorily the action of the velar folds. By adding ether occasionally one can control the rapidity of the respiratory movements so that they may be slow enough for careful study. For some purposes one may advantageously remove the entire head cephalad of the velum.

On a frontal section at the level of the branchiopores like the one shown in Pl. VIII, fig. 52, one can very readily see

the course of the water in its passage through the branchial apparatus.

With larvæ in confinement, whenever the water is insufficiently aerated, the head and sometimes the whole branchial apparatus is projected from the burrow into the water. If the water is changed they disappear in a short time. If the water is not changed or aerated in some way the larva will leave its burrow entirely and make violent efforts to escape from the vessel. If one watches the indications he soon learns about how often to change the water ; in any case he knows that the water must be aerated or changed whenever the larvæ give this sign of beginning suffocation.

Respiratory Mechanism in the Adult. — On the change from the larval to the adult form, the food changes from minute organisms filtered from the water to blood sucked from other fishes, and the mode of inspiration must necessarily change ; for when the lamprey is attached for the purpose of obtaining food or for any other object, there is no possibility of inspiring water through the mouth. When unattached, however, water may still be taken into the branchial cavity through the mouth. For a considerable time during transformation and even when the tongue and the mouth have nearly assumed the mature condition, if one watches the particles in the water it is seen that there is still an almost constant stream flowing into the mouth. Later, however, although water may enter the mouth in respiration, it does so rarely, but on the contrary both inspiratory and expiratory streams must pass in and out of the branchial chamber through the branchiopores.

As shown in figure 52 of Pl. VIII, the branchiæ of the larva appear to project freely into a common branchial chamber, although there are seven openings on each side from this chamber. In the adult, on the other hand, there are seven gill pouches on each side, each pouch being independent except for a small opening into the greatly constricted bronchus ; and, as stated above, the respiratory streams are both in and out of each branchiopore so that if the bronchus were entirely occluded and part of the gill pouches obliterated,

as sometimes happens, the respiration of the animal could still be carried on. In other words having 14 practically independent gill pouches renders the liability to suffocation far less than if a single entrance or exit served for the entire respiratory supply.

Since in the adult, the inspiratory stream must enter the same opening from which the expiratory stream emerges, there must be a different arrangement of valves from that obtaining in the larva, where the branchiopores serve only for the exit of the water. The single valve of the larva is present in the adult, but it is not wide enough to cover the entire branchiopore as in the larva; usually it covers only about the cephalic half (Pl. VIII, fig. 55).

Inspiration is effected largely in both adult and larva by the elasticity of the cartilaginous branchial basket-work, and expiration through the constriction of the branchial apparatus by muscular action, thus standing in marked contrast to the respiratory actions of mammals where the thoracic cage must be expanded by active muscular contraction for inspiration, while expiration is largely effected by the elasticity of the respiratory apparatus.

In the case of the lamprey one might think at first that no valves are necessary in respiration, for if the branchial pouches are open to the surrounding medium through the branchiopores any enlargement of the branchial space would cause the water to enter, and conversely, any constriction would empty the branchial sacs. This view is correct, but this mode of simply drawing water into a sac and expelling it has not apparently answered the requirements of the lamprey, and there is present the thin valve (the ectal valve) which covers the entire branchiopore in the larva (fig. 52–55), and in addition a double valve (ental valve) (fig. 55), which is formed by the growth and modification of the middle gill lamella of the caudal half of the branchial sac. This lamella, near the branchiopore, bifurcates and soon loses its secondary laminæ and each part extends laterad as a firm but flexible membrane attached to the caudal wall of the branchial sac, one to the dorsal the other to the ventral edge of the branchiopore and

also somewhat to the dorsal and ventral parts of the ectal valve. The other or the cephalic edge of each valve is free.

The action of the valves is as follows: In inspiration, the two parts of the inner or ental valve turn away from each other and are pressed toward the cephalic wall of the branchiopore across the channel at the edge of the branchial sac, and the ectal or transverse valve folds over the ental one. By the expansion of the branchial apparatus, the entrance to the gill sac has been rendered more direct and the inflowing stream flows directly into the sac (Fig. 53). In expiration, the water flows through the branchial lamellæ, while around the edges, *i. e.*, at the dorso- and ventro-lateral edges of the gill sac there is formed a canal or gutter by the shortening of the gill lamellæ. The free ends of the lamellæ are also membranous and curved and aid in making a very complete and smooth canal. The ental valves at the entrance to the branchiopore cross this canal and serve as a guide to the inspiratory stream, not allowing the water to get into the canal around the edges of the gill sac, but directing it into the gill sac itself (Fig. 53). In expiration, however, with the change in obliquity and the constriction of the gill sac, the water passes between the branchial lamellæ into the canal and meeting the ental valve rotates the two folds of the valve toward each other and against the caudal wall of the branchiopore, thus removing the obstruction in the canal and really extending it by means of the arched valves (Pl. VIII, Fig. 54, 55). From this arrangement it is seen that two distinct objects are attained, the water not only bathes the gills but passes between the lamellæ, it is then concentrated in a canal with smooth sides where the friction is at a minimum; and in its exit from the branchial sac in expiration, the valves prevent the used water from making a circle in the gills, and more important, they form a very oblique channel which directs the expiratory stream caudad, thus insuring the animal against using the same water over and over. In inspiration, on the other hand, from the direction of the opening, the water enters at nearly a right angle to the axis of the animal, and thus fresh or unrespired water is constantly supplied to the gills. (See figures 51–55, Pl. VIII).

While the branchial pouches are, as stated above, practically independent, nevertheless they do communicate through the common bronchus, and occasionally a particle entering the branchiopore of one side may be seen to emerge from the opposite branchiopore (Bert, '67). If one observes the respiration of a lamprey resting upon its side in very shallow water so that the branchiopores are near the surface, the oblique streams from the branchiopores are very readily seen. If the nostril is near the surface of the water a stream is seen to emerge from it at every expiration. Hence as the nasal sac is closed caudally, a stream must be drawn in at every inspiration and expelled at every expiration. This movement simply accompanies respiration and is not for respiratory, but rather for olfactory purposes. That there is no connection between the stream forced from the nostril and the respiratory water may be easily proved by raising the head slightly above the water. After the first expiration no further jets of water are sent from the nostril until the head is again submerged, thus showing that the water enters and emerges from the same opening.

All the respiratory movements may be artificially imitated on a lamprey soon after death, if the branchial apparatus remains expanded. To insure this the lamprey may be curarized; the branchial apparatus being unconstricted by the paralyzed muscles, expands by its own elasticity, and the animal will die in the inspiratory phase. If now the branchial apparatus is grasped by the hand the expiration may be imitated by constricting the apparatus and the streams from the branchiopores and from the nostril demonstrated. Upon relaxing the grasp the branchial apparatus re-expands and refills the gill pouches. By proceeding slowly, one can see with the greatest accuracy the movement of the branchioporic valves, and what is obscure, from the rapidity of action in the living state, becomes clear and intelligible.

THE BLOOD AND ITS FIBRIN, HEMAGLOBIN AND CORPUSCLES.

As in the higher vertebrates, the blood of the lamprey in all stages, except the very early embryonic ones is red in color

and contains both red and white corpuscles. This blood coagulates very quickly, and the fibrin is composed of exceedingly fine and also coarser filaments. If preparations of lamprey and human fibrin filaments are compared (Pl. VIII, fig. 44, 45), it will be seen that in both there are centers from which these filaments seem to radiate, and that in the lamprey, while there are coarse filaments, the ultimate net-work is almost inconceivably fine and that in order to define it well, homogeneous immersion objectives are necessary. On the other hand the net work of filaments in human and other mammalian fibrin is coarse. This condition has been found in all the mammalian fibrin examined, while the fine network seems to be characteristic of the cold-blooded animals.

The time required for coagulation in the lamprey is short, shorter than for mammalian blood but not nearly so short as for amphibian blood (Gage '90).

The hemaglobin of the lamprey is exceedingly difficult to obtain in crystalline form. The only successful efforts so far have been by using a considerable quantity of blood and adding at the edge of the cover a small amount of a 10 per cent. aqueous solution of pyrogallic acid. The cover is then sealed and put in the light in a cool place. After several days, in successful preparations, crystals appear in beautiful rosettes with frond-like rays radiating from the center.

The Red and White Blood Corpuscles.—It is to the solid constituents of the blood that the greatest interest attaches, and especially to the red-corpuscles; for "as the red blood-corpuscles of the camelidæ form an exception in the great mammalian group in being oval instead of circular in outline, and, according to Gulliver in not forming distinct rouleaux, or rolls, so the red corpuscles of the lamprey eels form an exception in the great non-mammalian group of vertebrates (birds, reptiles, and fishes) in being *bi-concave* and *circular*, instead of *oval* and *bi-convex*, like those of all other animals in this great group. The corpuscles also agree with those of mammals in forming distinct rouleaux. This is most marked in the brook lamprey and the larva. In the 9 mm. embryo the corpuscles were often seen in rolls of three or four in the

circulating blood (Pl. VIII, fig. 42, E. F.). Rouleaux have also been observed in the vessels of a living dog's mesentery. A nucleus is present in all the corpuscles, but as it is small and placed in the thickest part of the corpuscle, it is not apparent in the perfectly fresh ones, except faintly in some of those of the 9 mm. embryo. The corpuscles when fresh appear, therefore, almost exactly like those of man." So complete is the resemblance, that skilled observers have frequently been confused, and pronounced fresh preparations of lamprey's blood to be mammalian. As seen in the table, however, the number of the white corpuscles is proportionally very much greater than in mammalian blood, and the white corpuscles are almost always smaller than the red ones, thus standing in these two particulars in marked contrast with mammalian blood. Furthermore "no element of uncertainty should arise with respect to them in legal medicine, for (*a*), the presence of a nucleus may be readily demonstrated, as it is made apparent by drying, by acetic acid, and by the reagents most used in examining blood for medico-legal purposes; (*b*), except in the embryo 9–10 mm. long, the corpuscles are nearly twice as large as those of man. (Compare the accompanying table of measurements). Hence the red blood corpuscles of lamprey eels, in spite of their bi-concave form and circular outline, really offer no more difficulty in medical jurisprudence than do the corpuscles of any other of the non-mammalian vertebrates.*

"The circular outline of the red blood-corpuscles in both adult and larval lampreys was discovered by R. Wagner and the fact published in 1838 ('38). The bi-concave character is remarked upon by Wagner, Kölliker, and others, but I have seen no reference to the fact that the corpuscles form distinct rouleaux like those of mammals. This feature, as in mammals, is lost soon after death.

"Although the bi-concave character of the corpuscles of lampreys is as easily demonstrated as in the corpuscles of

* While it is true that the red corpuscles of mammalian embryos and the developing corpuscles in the adult are nucleated, the size and uniformly nucleated condition of the corpuscles of the lamprey would sufficiently characterize them.

mammals, it is stated by Gulliver and Günther that they are flat or bi-convex, and Gegenbauer in his Comparative Anatomy, states that the red blood-corpuscles of birds, reptiles, amphibia, and fishes are bi-convex, no exception being made for the lampreys. Parker in his translation of Wiedersheim's Comparative Anatomy of the Vertebrates, says: 'In case of the red corpuscles, the nucleus persists, and the whole cell is bi-convex in all vertebrates below mammals.' In 1887 wide circulation was given to a statement by Shipley ('87), and Thompson ('87), that the red blood-corpuscles of larval lampreys were oval in outline, like the rest of the non-mammalian vertebrates."

And Thompson further adds: "The noteworthy point now is, that myxine possesses red corpuscles similar to those, not of the adult, but of the larval lamprey, which in many ways it resembles otherwise." On consulting the original article by Shipley ('87), the statement is found to be: "The blood corpuscles are of only one kind, large oval disc-like structures, with a well-marked nucleus." The size of the embryo is not given, but it was in the stage before the white blood-corpuscles appear. As all observers have noted the tendency of the red corpuscles to become deformed, one can readily understand that, if the form were observed in sections, from mutual compression the corpuscles would not remain of circular form. If Dr. Shipley examined these corpuscles in the serum of the larva and in the living condition, and they were found oval instead of circular, the fact would be exceedingly interesting and perhaps suggestive. One would hardly expect to find embryonic blood-corpuscles oval, for even in animals in which the red corpuscles of the adult possess an extreme elliptical form the embryonic ones are either circular or approximately so (Kölliker '84. Milne-Edwards).

"That the red blood-corpuscles of both the adult and larval lampreys are circular, bi-concave, nucleated discs, as here described and figured, was repeatedly demonstrated in larvæ from 9 to 142 mm. long, and in numerous adults. In every specimen examined all the corpuscles not irregular were circular in outline. To make sure that this appearance was not

due to reagents, the corpuscles were examined in the serum of the blood, without the addition of any reagent whatever, and to avoid any possible error on account of the small amount of blood in the 9 mm. embryo, the circulating blood was examined. All the examinations were made with a 2 mm. apochromatic objective and an ocular × 12 " (Gage '88).

Table showing the diameter and thickness of the red and of the white blood-corpuscles of the lamprey in the adult and larval condition; also the relative number of red and white corpuscles, and the number of red corpuscles in a cubic millimeter of blood.

	DIAMETER. *Red.*			Thickness.	Ratio of thickness to diameter	Ratio of white to red corpuscles.	No. of red corpuscles in a cubic millimeter.
	Maximum.	Minimum.	Average.				
Lake lamprey (June),	16.16μ	10.1 μ	14.2 μ	5.05μ	1 : 2.8	Male, 1 : 20 Fem., 1 : 15	Male, 391,333 Fem. 334,666
Lake lamprey (Oct.),	16.25μ	10.62μ	13.9 μ	5.0 μ	1 : 2.78	Male, 1 : 17	Male, 513,280
Brook lamprey (May),	15.15μ	10.1 μ	13. μ	5.02μ	1 : 2.59	1 : 95	500,000
Larval lamprey, 142 mm. long,	15.65μ	12.12μ	13.4 μ	3.48μ	1 : 3.8	1 : {4 / 30	712,950
Embryo lamprey, 9 mm. long,	8. μ	7. μ	7.448μ	1.96μ	1 : 3.8	1 : 10	Not determined.
		White.					
Larval lamprey, 58 mm. long,			5.56μ				
Lake lamprey (Apr.),			7.8 μ				

The blood for measurement and counting was taken from the heart of an animal just killed or from a pithing wound, and mounted without the addition of any liquid. The coverglass was supported by a hair and sealed with castor oil. Only undistorted corpuscles were measured. The averages were obtained from twenty-five measurements in each case. All measurements were made with a $\frac{1}{12}$ or $\frac{1}{18}$ homogeneous objective, and a Jackson ocular micrometer, the valuation of which was determined by using a Rogers' standard stage micrometer.

In a larva 73 mm. long, the average diameter was 12.44μ—that is, 0.96μ smaller than in the larva of 142 mm. given in the table. Gulliver ('62–'75, p. 845) states that there is little difference between the blood-corpuscles of *Petromyzon planeri*, *P. fluviatilis*, and *Ammocœtes branchialis* [the larval form]; that one description may serve for all three of them; and gives the following measurements: Diameter of the red corpuscles, 11.9 μ; thickness, 4.09 μ; diameter of nucleus, 3.96 μ. Köl-liker gives 11.3 μ as the size, not mentioning the species or the age. Welcker ('63), gives 15 μ as the average size of the red corpuscles of *Petromyzon marinus*, with a maximum of 16 μ and a minimum of 13.4 μ. Thickness of the corpuscles, 3 μ. For the larva the average is 11.7 μ, with a maximum of 12.4 μ and a minimum of 10.9 μ. Thompson ('87), gives the size of the red corpuscles of *Petromyzon marinus* as 13 μ to 14 μ. Welcker gives the number of red corpuscles in a cubic millimetre of the blood of *P. marinus* as 133,000.

In my own studies, which have extended through several years and have considered specimens at various seasons, the statements of Gulliver are not wholly verified. On the other hand, as shown in the table, the red corpuscles increase in size with the increase in size of the whole animal. This is most marked in larval life. After nearly reaching their full growth as larvæ the increase of the red corpuscles to the fully adult condition is only about one micron (1 μ), while between the 9 mm. and the 73 mm. larva there is a difference of 5 μ. but only about 1 μ. between the 73 mm. larva and the one 142 mm. long. This fact of the growth in size of the corpuscles with the growth in the size of the body is again in marked contrast with what is known of the mammalian red corpuscles, which in the new born and the fully matured differ very little in size.

The relative number of red and white corpuscles has been determined at various seasons of the year, and while the number of white ones is greater in some specimens than in others, the season does not seem to affect this ratio very markedly. In general, the lake lamprey has a greater relative number of white ones than the brook lamprey, and in the larva they are more numerous than in the adult. In no case was there seen

the proportion given by Thompson, *i. e.*, three or four white ones to one red one. In my own observations the red ones were always in excess of the white ones. (See table above).

The amœboid movements of the white ones are striking and vigorous in both larva and adult, but as a rule the motion does not begin immediately after the preparation is made. It is usually at its greatest about half an hour after the blood is obtained.

SUMMARY AND GENERAL CONCLUSION.

1. Two species of lampreys inhabit the chain of lakes in western New York.

2. One, the brook lamprey (*Petromyzon* or *Ammocœtes branchialis*) is small in size, few in numbers and short-lived, in the adult stage. It is not known in North America outside the Mississippi Valley except in the Cayuga Lake basin. It is probably widely distributed, but from its small numbers and inconspicuous coloring, it has been overlooked (Plate IV, pp. 436, 452).

3. The other, the lake lamprey *Petromyzon unicolor* or *dorsatus*), is of large size, is in great numbers and lives a parasitic life in the lakes for a period of two to three and one-half years, and perhaps longer (Plate I, III, pp. 431, 445, 452).

4. The lake lamprey from the structure and arrangement of its teeth is hardly to be distinguished from the true anadromous sea lamprey, but judged by the physiological test of natural interbreeding it must be considered as specifically distinct (Plate VI, p. 426).

5. Both species have a larval stage and a metamorphosis at the end of from two to four years. Thus agreeing with the Petromyzontidæ wherever thoroughly studied (Plate III, IV, VI, VIII, pp. 449, 452).

6. The proportions of parts of the body with the two sexes of the lake lamprey, are very unlike and mutually interchange between the ordinary non-breeding and the breeding season. (See Table and p. 431).

7. In both species there are striking atrophies and hypertrophies at the spawning season (Plate III, IV, VII, p. 438).

8. Both species construct similar nests for the deposit and

protection of the ova. The larvæ hatch in these nests, remain there till they are about 12 to 15 millimeters in length, then they seek a sand bank in the concavity of the stream. In this bank they remain until fully transformed and supplied with horny teeth. They then leave the sandy covering and lead a roving, parasitic life in the open waters of the lake (Plate VII, VIII, pp. 441, 449).

9. In its larval life the lamprey is not injurious to man, but aids him by serving as bait for food fishes (p. 457).

10. During adult life the lamprey is highly injurious, as it preys upon food fishes. The lake lamprey is the more injurious from its larger size, greater numbers and longer parasitic life (pp. 445, 457).

11. The lakes could be easily freed from lampreys, by catching and destroying them when they are on their way to the spawning grounds up the lake inlets (p. 461).

12. The respiratory mechanism of the lamprey is very perfect at all stages. From the perfection and arrangement of the branchial valves, the expired water is not re-inspired (Plate VIII, pp. 463, 467).

13. The blood-corpuscles are of two kinds, white and red as in most other vertebrates.

14. The white blood-corpuscles are relatively more numerous than in mammalian blood; they are mostly smaller than the red blood-corpuscles and exhibit active amœboid movements (Plate VIII. p. 471).

15. The red blood-corpuscles are bi-concave, circular discs as with mammalian blood-corpuscles, and like the mammalian red blood-corpuscles those of the lamprey arrange themselves in rolls or rouleaux, (Plate VIII, p. 472).

It is assumed throughout this paper that the lake lamprey is a land-locked species which is a recent offshoot from the true anadromous sea lamprey. But for the very striking similarity, a similarity amounting almost to specific identity with the sea lamprey, one might be strongly inclined to the belief that the lake lamprey is an original product of the lake waters and has only a remote relationship with the sea lamprey through some primitive and common ancestor. On the other hand it might be urged that as there is free communication between

the lakes and the ocean through the St. Lawrence River, there is no occasion to consider the lake lamprey as a land-locked form at all.*

While it is true that the natural obstacles are not such as to prevent the immature lampreys from passing to the ocean and then returning when mature to deposit their spawn, the distance inland is greater than undoubted sea lampreys have ever been known to pass; certainly none have ever been found in Cayuga and Seneca lakes by the writer, and from information obtainable from others none have been seen in any of the lakes or in Lake Ontario.†

The final and definite proof that the lake lampreys remain permanently in the lakes and do not go to the ocean at any time, has been abundantly obtained during the past 18 years by the capture of examples of the adult form of all sizes in the waters of the lake during every month of the year, while the true anadromous forms are found in the inland waters they are known to inhabit, only when very small and when spawning.

As to a reasonable hypothesis for the presence of these isolated or land-locked lampreys: It is recognized by all modern geologists and physical geographers that the present contour of the country and the details of the topography of the greater and lesser lake basins with their water courses and ridges are, geologically speaking, only of recent date. .By glancing again at the small topographical map (Pl. II) it can readily be seen that during the glacial epoch when the basins of the St. Lawrence and of the lakes were filled with ice, the water from the melting ice accumulated and finally passed the low elevation south of the lake basin and found its way to the Susquehanna River. Later, as the ice sheet receded, the outlet was through the Mohawk into the Hudson River. Finally

* The common eel (*Anguilla rostrata*) is also abundant in the lakes. As it has been determined by recent investigations that the common eel goes to the ocean or to brackish water to spawn and the young return to fresh water to mature, it will be seen that the passage to and from the ocean is not insuperable.

† I wish to express my indebtedness to the State Game and Fish Protectors who so fully and courteously answered the questions concerning the lampreys of their respective districts.

as the ice melted the superfluous water of all the lakes gradually found an exit through the St. Lawrence basin as it had done in pre-glacial times.

The application of these geological or topographical changes would have the following bearing upon the special subject of this paper. At the present time in the Susquehanna River, only a few miles to the south of Cayuga Lake, the large sea lampreys are found in the summer or spawning season and the transforming ones in the autumn, and larvæ during the entire year, thus showing that even at the present day the large sea lamprey uses the Susquehanna for a spawning ground. The same is true of the Hudson River.

Now it is believed that while the lakes poured their superfluous waters southward into the Susquehanna River that the large sea lampreys frequented the lake and its tributaries and found suitable spawning grounds. As the glacier receded and the streams draining the lake into the Susquehanna became shallower and more difficult to ascend and descend, the lakes were less and less and finally no more visited by the spawning lampreys; and some of the newly transformed ones, finding abundant food in the common fishes which swarmed in the waters, remained and matured in the lakes, and spawned in its tributaries thus completing the entire life-cycle in fresh water.

It is also possible that as the water courses to the Susquehanna decreased and those to the Mohawk and Hudson increased, the lampreys entered and left the lake through those streams, but ultimately the same result would follow and the forms become isolated in the lakes.

If it is granted that the presence of the lake lampreys can be satisfactorily accounted for in the way described, it is not difficult to conceive of the diminiution in size and perhaps also of the other modifications, as the great increase of the dorsal ridge in the male; for it is within human observation that sea animals that have been artificially or naturally isolated from the ocean gradually decrease in size, and that special features may become accentuated or intensified.

ITHACA, N. Y.
September, 1893.

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'**61**. OWEN, R. Comparative Anatomy and Physiology of vertebrates. 8°, 3 vols., London, 1861–1868. Vol. I., 1861.

'**82–83**. PARKER, W. K. On the skeleton of the marsipobranch fishes, part 2, Petromyzon. Proc. Roy. Soc., 1882, pp. 439–443; 1883, pp. 1–3; Philos. Trans. Roy. Soc. part 2, 1883, pp. 373-457.

'**84**. PARKER, T. J. A course of instruction in Zootomy, Vertebrata. 8°, pp. 397. London and New York. Good account of the anatomy of the adult lamprey.

'**88**. ROLLESTON, G. Forms of animal life, a manual of comparative anatomy with descriptions of selected types. Second edition, revised and enlarged by H. W. Jackson. pp. xxxii + 937. Oxford. "At the metamorphosis the tubular structure [of the liver] is lost; fat appears in the cells; the gall-bladder, and bile duct are absorbed. . . . . The pancreas is perhaps represented in the lampreys by an acinous gland opening into the widened commencement of the mid-gut on the left side" (p. 435).

'**79**. SCHNEIDER, A. Beiträge zur vergleichenden Anatomie und Entwicklungsgeschichte der Wirbelthiere. 4°, pp. 164. Berlin. Discusses the habits, structure and transformations of lampreys.

'**81**. SCOTT, W. B. Beiträge zur Entwickelungsgeschichte der Petromyzonten. Morph. Jahrb., VII, pp. 101–172.

'**87**. —— Development of Petromyzon. Jour. Morph., I. pp. 253–310. The myel is rounded in the embryo, flattens before adult life.

'**86**. SEELEY, H. G. The fresh water fishes of Europe; history of their genera, species, structure, habits and distribution. 8°, pp. 444; London, Paris, New York and Melbourne.

'**87**. SHIPLEY, A. E. On some points in the development of *Petromyzon fluviatilis*. Quar. Jour. Micr. Sci., XXVII, pp. 325–370. On p. 343 he says that in the embryo there is but one form of blood-corpuscle and that this is "large, oval and disc like."

'**87**. THOMPSON, D'ARCY, W. On the blood corpuscles of the Cyclostomata. Ann. and Mag. Nat. Hist., Ser. V, Vol. XX, pp. 231–233; Anat. Anz., II, pp. 630–632.

'**38**. WAGNER, R. Beiträge zur vergleichenden Physiologie, Vol. II, 1838. Nachträge zur vergleich. Physiol. des Blutes, p. 13. First announcement that the red blood corpuscles of larval and adult lampreys are circular and biconcave.

'**63**. WELCKER, H. Grösse Zahl, Volum, Oberfläche und Farbe der Blutkörperchen bei Menschen und bei Thiere. Zeit. f. ratl. Med., 3d Reihe, XX, pp. 257–307.

EXPLANATION OF THE PLATES.

Plates I, III, IV, and V are from photographs of fresh or preserved specimens. The specimens in most cases were immersed in water or alcohol, and photographed with a vertical camera. Plates VI, VII, and VIII were drawn by Mrs. Gage from photographs or from the object by the aid of a camera lucida.

PLATE I. FIG. 1–2.

A pair of lake lampreys about 33 centimeters long, from the same nest; obtained June 9, 1893. At the head of the article.

FIG. 1. Male lake lamprey showing dorsal ridge and the approximation of the two dorsal fins. This specimen weighed 101 grams.

FIG. 2. Female lake lamprey. The dorsal fins are not connected, and no dorsal ridge is present, but the anal notch is marked. This female had almost completed spawning, and hence appears slender. Compare with the sea lamprey full of eggs (Fig. 17, Pl. V).

The stone to which the specimen is attached weighed 199 grams, the specimen only 72 grams. While this pair were in the nest and under observation the female was seen to drag this stone down the stream for a considerable distance.

PLATE II. FIG. 3-4.

Map of the head of Cayuga Lake, showing the surrounding country and the streams flowing into the lake. (From W. R. Dudley's Cayuga Flora.) The squares on the map are kilometers and the zero point is the University Signal Station (U. S. S.) point of reference, a point on the University campus, whose latitude and longitude have been determined with great accuracy by the Department of Civil Engineering. Fig. 4, in the upper right hand corner, is a topographical map of the lake basin designed especially to show the lakes and their outlet through the Oswego River, the water-shed around the basin is indicated by interrupted lines, and also the water courses draining the elevation surrounding the lake basin. It is to be noted that the Susquehanna River with its tributaries is the most important of these.

There is an important ridge between Lake Ontario and the interior lake basin, and this elevation is drained by numerous small streams flowing northward into Lake Ontario. It is to be especially noticed also that this elevation is broken through by the Oswego River.

L. Lake; *R.* River; *Cnd.* Canandaigua Lake; *Crkd.* Crooked or Keuka Lake; *Owsc.* Owasco Lake; *Sktls.* Skaneateles Lake; *Ond.* Onondaga Lake. Several small lakes have been omitted.

PLATE III. FIG. 5–10.

Figures to represent the relations of the two dorsal fins in the male lake lamprey in and out of the spawning season, the female in the spawning season, and two larvæ of very different sizes.

FIG. 5. (About ½d natural size). The first lake lamprey obtained. The branchial apparatus is in the inspiratory phase, and therefore widely expanded. The dorsal ridge, so characteristic of the male lake lamprey, is more than usually prominent in this specimen; the fusion of the two dorsal fins is also shown.

FIG. 6. (⅓ natural size). Part of a male lake lamprey caught in December, to show the decided interval between the two dorsal fins; also to show the non-appearance of the genital papilla out of the breeding season. The myotomes are also very clearly indicated.

FIG. 7. (⅓ natural size). Segment of a male lake lamprey in the spawning season, to show that the two dorsal fins appear continuous or simply notched during this season. The genital papilla is also very prominent at this period.

FIG. 8. (⅓ natural size). Caudal end of a female lake lamprey in the spawning season to show the separation of the dorsal fins even in the breeding season in the female; the notched appearance of the vent and the fin-like fold extending to the caudal fin.

FIG. 9. (Natural size). The caudal half of a larval lamprey 150 millimeters in length, to show the separation of the two dorsal fins. The myotomes are also well shown in part of the length.

FIG. 10. (Natural size). A small larval lamprey to show the separation of the dorsal fins even in specimens of this size. In specimens only 40 mm. long, there is a notch in the fin showing plainly where the interval is to be.

PLATE IV. FIG. 11–15.

Brook Lampreys and a larva just before transformation.

FIG. 11–12. (Natural size). A pair of brook lampreys taken at the spawning season. Photographed under water with a vertical camera. The male (Fig. 11), has a somewhat prominent genital papilla. In the female (Fig. 12), there is present a marked anal fin-like fold, and the caudal part of the abdomen is full of eggs. In both male and female there is a notch, but no interval between the two dorsal fins, and in the female the cephalic part of the second dorsal is edematous. Compare figure 14.

FIG. 13. (Natural size). The caudal part of a brook lamprey that had just transformed. The specimen was taken in October, and measured 200 millimeters in length. The two dorsals are widely separated, but appear to be connected by a very low ridge.

FIG. 14. (Natural size). An oblique view of the caudal part of a female brook lamprey especially to show the edematous second dorsal fin, filling, almost completely, the notch between the two dorsals. Near the end of the spawning season this edema is frequently infiltrated with blood so that the females are marked by a bright scarlet spot.

FIG. 15. (Reduced $\frac{1}{18}$th). Larval lamprey, 190 millimeters in length, to show the size the larvae may reach before transformation. This one is longer than the adult brook lampreys here figured, but not quite so long as the one from which figure 13 was taken.

PLATE V. FIG. 16–18.

A pair of sea lampreys, from Lawrence, Mass., running up the Merrimac River to spawn. Photographed under water after preservation in Müller's fluid.

FIG. 16. (About $\frac{1}{3}$d natural size). A male sea lamprey 575 millimeters long at the spawning season. The dorsal ridge is very low and the two dorsals are separated by a considerable interval. The eyes were sunken and obscured during the preservation.

FIG. 17. (Somewhat less than $\frac{1}{3}$d natural size.) A female sea lamprey 645 millimeters in length at the spawning season. The eggs had not yet been shed, hence the fullness of the abdomen. Opposite the first dorsal fin the roundish white mark indicates the place where another lamprey had attached itself to this one. The incompleteness of the tail on the ventral margin is due to some accident either before or after death.

FIG. 18. (Natural size). Ventral view of the head of the male lamprey shown entire in figure 16. To show the arrangement of the sensory or nerve papillae (see Fig. 20 and 51, Pl. VI and VIII). The circumoral fringe or plaiting and the lateral closure of the mouth are also shown. The oblique direction of the branchiopores is shown, especially on one side.

PLATE VI. FIG. 19-26.

The mouth and its appendages in the adult, transforming and larval stages. The figures of the adult mouths are from photographs of the fresh specimens made during the spawning season. The other figures are from camera lucida drawings of preserved specimens. The magnification of each is given immediately after the number of the figure.

FIG. 19. (× 2). The ventral aspect of the head of a lake lamprey especially to show the arrangement and number of the teeth. By comparing the teeth of the supra- and infra-oral laminae with those of the annular cartilage from another specimen (Fig. 24), it will be seen that there are 9 infra-oral teeth on the annular cartilage, and 8 in Fig. 19. The range is from 6 to 10, the most common number being 7 or 8. In rare cases the two supra-oral teeth are fused, thus giving the appearance of a single median tooth.

E. Eye.

S. O. Sense organs or nerve papillae. For those on the lateral and dorsal aspect of the body, compare figure 51 of plate viii.

FIG. 20. (× 2). Ventral aspect of the head of a sea lamprey from Lawrence, Mass., to show the oral disc with its concentric rows of teeth, the supra- and infra-oral teeth and the teeth of the tongue. Compare figure 25.

S. O. Sensory organs or nerve papillae.

FIG 20, *A-E.* (× 5). Enlarged papillae from the circumoral fringe, to show their size and form at different parts of the circumference. In the lake lamprey the papillae are almost exactly like those here shown, not differing more than the papillae in different sea lampreys.

A-B. From the fringe at the meson and the cephalic edge of the disc.

C-D. Papillae from the side of the disc.

E. Papillae from the meson at the caudal side of the disc.

FIG. 21. (× $3\frac{1}{4}$). Ventral aspect of the head of a brook lamprey to show the number and arrangement of the teeth. The body opposite the gills is enlarged, as the photograph was taken during the inspiratory phase. The whole dentition is seen to be weak as compared with the lake or sea lamprey. The lingual tooth plate is also markedly different.

E. Eye.

S. O. Sensory organs or nerve papillae.

A–C. (× 12.) At the left. Papillae from the circumoral fringe of the brook lamprey. *A* is from the meson at the cephalic edge, *B* from the side, and *C* from the meson at the caudal edge of the disc.

FIG. 22. (× 16). Ventral view of the head of a larval lamprey 135 millimeters long to show the ventral lip, the upper or dorsal hood-like lip, and the branched tentacles forming a sieve over the entrance to the mouth. In this figure the tentacles are somewhat unnaturally separated. During life they are more closely approximated, thus making a fine strainer to prevent the entrance of coarse particles into the branchial cavity. By comparing with figure 41 of plate vii, the entire tentacle will be seen to resemble a cauliflower somewhat.

D. L. Dorsal lip or hood. It embraces the lateral extensions of the ventral lip.

L. T. The ventral median tentacle which may be designated the *lingual tentacle* as it is supposed to be an important factor in the formation of the adult tongue.

V. L. Ventral lip. Its lateral extensions are entad of the dorsal lip.

FIG. 23. (× 16). Ventral view of the head of a transforming larva, to show the narrowing of the head and mouth at this stage, and also the arrangement of the tentacles around the oral disc, as if they were to be transformed into the future teeth. The union of the dorsal and ventral lips to form the circular, oral disc is also shown.

D. L. and *V. L.* The dorsal and ventral lips in the process of fusing.

L. T. The tongue which appears to be derived largely from the median lingual tentacle. Compare figure 22.

FIG. 24. (× 3). Annular cartilage of a lake lamprey, to show the form of the cartilage and the position of the supra- and infra-oral teeth.

F. Foramen opening into the interior of the cartilage. There is something of an angle at the point of entrance of the foramina and the general appearance is strikingly like the jaws of a shark.

I. L. Infra oral or mandibular teeth. There were nine in this specimen, eight in the one represented in figure 19.

S. L. Supra-oral lamina or maxillary teeth.

FIG. 25. (× 2½). Annular cartilage and part of the tongue with the lingual teeth of a sea lamprey. The tooth plates are removed from the annular cartilage, thus bringing into view the supporting eminences of cartilage for each tooth.

F. Foramen near the middle of the annular cartilage.

I. L. Infra-oral or mandibular tooth supports.

L. T. Lateral lingual teeth. There are thirteen on the right and but ten on the left. Ordinarily the lateral variation is not so marked.

S. L. Supra-oral or maxillary tooth supports.

T. Part of the tongue.

V. L. Ventral lingual lamina. Compare the ventral lingual tooth-plate in figures 19–20, and 21.

FIG. 26. (× 7). Annular cartilage of the brook lamprey.

F. Foramen leading to the interior of the cartilage. Compare the same in figures 24, 25.

I. L. Infra-oral lamina supported by the ventral half of the annular cartilage.

S. L. Supra-oral lamina or maxillary tooth-plate supported by the dorsal half of the annular cartilage. This plate is in marked contrast to those of the lake and sea lamprey, where the maxillary teeth are very close together. Brook lampreys are occasionally found with one or more intermediate teeth on the supra-oral lamina. (Jordan, '82, '85.)

PLATE VII. FIG. 27–41.

A series of transections near the middle of the body to show the changes in the gonads (ovary and spermary) at various stages of growth; atrophy of the intestine in the breeding season; nest building, and the oral tentacles and velar fold of a larva. The scale is indicated after the number of each figure.

Structures appearing in all the transections, all abbreviations on Fig. 27.

A. Aorta.

C. V. Cardinal veins.

G. Gonad. The reproductive gland (ovary in the female, spermary in the male.) *G.* On each section. The ovary and testis are single, foliated organs in the lamprey, and are supported by a fold of peritoneum, Mesogonad, frequently called mesorchium in the male, mesoarium in the female.

I. Intestine. *I.* On all sections.

IM. L. Intermuscular ligaments between the myotomes.

K. Kidney and ureter.

M. Y. Myel, or spinal cord.

M. A. Mesenteric artery.

M. G. Meso Gonad. The duplicature of peritoneum supporting the ovary (*mesoarium*) or spermary (*mesorchium*).

M. P. Muscle plates cut transversely. *M. P.* on Fig. 27, and 36. Each myotome is made up of a multitude of muscle-plates or lamellae, each in a delicate connective tissue-sac. Only the empty sacs are shown in the figures.

M. T. Myotome or myomere. These overlap like tiles, so that in a transection of the body the cut ends of several appear. The overlapping myotomes are connected by the intermuscular ligaments (*IM. L.*).

M. V. Mesenteric vein. The mesenteric vein and artery are in the typhlosole.

N. Nucleus. On Fig. 29 A.

NC. Notochord.

T. Typhlosole, or spiral intestinal valve; letter on Fig. 27 and 37. The tissue of the typhlosole appears to be largely lymphoid in character. In the figures of the larva, the typhlosole is shown clearly to be a linear invagination of the intestine, thus forming a ridge. Commencing somewhat cephalad of the base of the left dorsal fin, the typhlosole or spiral valve extends cephalad as a right-spiral, and caudad as a left-spiral.

FIG. 27. (× 2½). Transection of an adult male lake lamprey taken in December, to show the size and appearance of the spermary about six months before the spawning season. The intestine also shows the size and general structure in the feeding specimens.

FIG. 27, *A*. (×53 and 700). A. Sperm mother-cell showing the multitude of sperm-cells within it. *B*, *C*. Individual sperm-cells magnified 700 diameters, to show their structure and appearance. In *B*, from an osmic acid preparation, two black spherules are shown in the darker part. *D*, A red blood-corpuscle with its eccentric nucleus, at the same magnification as *B*, *C*, to show the relative size of sperm-cells and red blood-corpuscles.

FIG. 28. (× 20). Figure of the edge of a lamella or lobule of the spermary, from the same specimen as figure 27, to show the appearance of the sperm mother-cells by reflected light. By comparing with figure

30 one can readily see the difficulty in distinguishing spermary and ovary. When properly prepared and viewed as transparent objects, however, the difference between the sperm mother-cells and the ova is most striking.

FIG. 29. (× 2½). Transection of a female lake lamprey taken in December, *i. e.*, about six months before spawning. To show the size of the ovary and of the intestine; compare description of Fig. 27 and 28.

FIG. 29 A. (× 53). A single ovum from the ovary of the same specimen as figure 29. To show the comparative size and general character of the ovum, with its eccentric nucleus; also to compare with a sperm mother-cell of the same stage of development. Compare Fig. 27 A.

FIG. 30. (× 20). End of a lobule of the ovary of the same specimen as figure 29. To show the general appearance of the ovary and ova about six months before spawning. Also the similarity in appearance of ovary and spermary at this stage of maturity. Compare Fig. 28 with its description.

FIG. 31. (× 2½). Transection of a male lake lamprey in the breeding season, to show the relative size of spermary and intestine, and for comparison with the spawning female (Fig. 32), and the non-spawning male (Fig. 27), also the enormous dorsal ridge appearing in the male lake lamprey during the breeding season.

D. Dorsal ridge.

FIG. 32. (× 2½). Transection of a female lake lamprey in the spawning season. Some of the ova are free. Compare with the non-breeding female (Fig. 29), and the breeding male (Fig. 31). While in the male the spermary is considerably larger at the breeding season, the ovary has far more strikingly increased in size.

FIG. 32 A. (× 53). Ovum of the spawning lake lamprey. The nucleus is obscured by the great amount of food-yolk. This figure is of the same magnification, and is introduced for comparison with figures 29 A, 34 A, 36 A, and 38 A, to show the difference in size of the ovum at various stages of maturity. It is also at the same magnification as the sperm-mother cells shown in fignres 27 A, and 35 A.

FIG. 33. (× 6). Transection of a just transformed male lake lamprey taken in October, and about 150 millimeters in length. To show the size of the spermary and of the intestine, and for comparison with a female at this stage (Fig. 34).

FIG. 34. (× 6). Transection of a just transformed female lake lamprey, about 150 millimeters long, taken in October. To show the ovary and intestine, and for comparison with the male at this stage (Fig. 33), also with the female brook lamprey (Fig. 36).

FIG. 34 A. (× 53). Ovum from the same specimen as figure 34. To show the size of the ovum at the time of transformation, and for comparison with the ovum of a brook lamprey at the same stage (Fig. 36 A), also with a larva (Fig. 38 A).

FIG. 35. (× 6). Transection of a just transformed male brook lamprey, about 190 millimeters long, caught in October. To show the intestine and the spermary, and for comparison with the just transformed female brook lamprey and the lake lamprey at the same stage (Fig. 33, 34). It will be noticed that the intestine is relatively smaller than in the just transformed lake lamprey.

FIG, 35 A. (× 53). Single sperm-mother cell of the just transformed brook lamprey, from the same specimen as figure 35.

FIG, 36. (× 6). Transection of a female brook lamprey, about 190 millimeters in length. Just transformed ; caught in October. For comparison with the male (Fig. 35), and with the female lake lamprey at the same stage (Fig. 34). It will be seen that the brook lamprey's ovary is much nearer maturity than is that of the just transformed lake lamprey.

FIG. 36 A. (× 53). Ovum from the ovary of the same specimen as figure 36. To show the size of the ovum in the just transformed brook lamprey, and for comparison with the lake lamprey (Fig. 34 A). It will be seen that this ovum is even larger than the one from the ovary of a lake lamprey six months before spawning (Fig. 29 A). From the appearance of sexual maturity it is believed that the brook lamprey spawns the spring following its transformation.

FIG. 37. (× 6). Transection of a larval male lamprey, 140 millimeters long ; caught in November. To show the small spermary and the intestine with a crescent-shaped lumen, due to the intruding typhlosole or valve ; no secondary folds are present as in the adult.

FIG. 38. (× 6). Transection of a larval female lamprey, 150 millimeters long ; taken in November. To show the ovary with the ova and the intestine. It was not cut at the same level as figure 37, hence the spiral valve or typhlosole occupies a different position.

FIG. 38 A. (× 53). Ovum from the ovary of the same specimen as figure 38.

FIG. 39. Section of a lake lamprey's nest with a pair of lampreys. The nest is sectioned parallel with the stream ; it is represented in the usual place for a lamprey's nest, just above ripples.

The female lamprey is represented as moored to a large stone, while the male is backing down stream carrying a stone of considerable size. It will be readily seen that disturbance of the stones at the upper edge of the nest would loosen the sand, and that it would be washed down stream and thus tend to fill the bottom of the nest, as shown. Mingled with the sand at the bottom of the nest are seen numerous ova, indicated by white circles.

FIG. 40. Face view of a creek with two lamprey nests just above ripples. In one nest two lampreys are indicated and in the other but one. In the concavity of the stream, where the water flows somewhat slowly, there is shown a deposite of sand and mud. It is in such situations that the larvæ live after leaving the nest.

FIG. 41. (× 8). A medisection or median sagittal section of a larval lamprey, 135 millimeters long. To show the oral tentacles, one side of the velum, and the relation of the velum to the branchial chamber. To be compared with the frontal section shown in figure 52, Plate VIII.

B. R. Branchiæ. They occupy a common chamber. The B. R. is on the third gill.

D. L. Dorsal lip or hood. Nearly its entire substance is muscular.

N. Single nasal opening.

N. C. Notochord.

V. L. Ventral lip.

VELUM. The right half or fold of the velum. There is a similar one in the left half of the body. Compare with figure 52 of Plate VIII.

PLATE VIII.

FIG. 42. (× about 1000). Red Blood-Corpuscles of lake, brook and larval lampreys. (From the *New York Medical Journal*).

A. Red blood-corpuscles of the lake lamprey. *a*, face view of a corpuscle; *b*, optical section of a corpuscle on edge; *c*, face view of a corpuscle, showing the nucleus after the action of one per cent. acetic acid; *d*, cup-shaped corpuscle.

B. Red blood-corpuscles of the brook lamprey. *a*, *b*, *c*, the same as in *A*.

C. Red blood-corpuscles of a larval lamprey 142, mm. long. *a*, *b*, *c*, as in *A*.

D. Red blood-corpuscles of a larval or embryo lamprey, 9 mm. long. *a*, *b*, *c*, the same as in *A*.

E. Rouleaux of the corpuscles of the brook lamprey in optical section. In the lower corpuscle a nucleus is indicated to show that it is small and in the thickest part of the corpuscle. It is visible only after the hemoglobin is partly or wholly removed from the corpuscle. In the embryo, where the corpuscles are so small, the nucleus is faintly visible in many corpuscles before the removal of the hemoglobin.

F. Rouleaux of the 142 mm. larva focused on the upper surface. In both *E.* and *F.* the corpuscles are shown of different sizes. Compare the maximum and minimum diameters in the table of measurements.

FIG. 43. (× about 1000). A single white blood-corpuscle in various amœboid phases, drawn freehand within two minutes.

FIG. 44. (× about 1000). Fibrin filaments of a larval lamprey. The filaments seem to radiate from centers, the centers appearing like white blood-corpuscles. Some of the filaments are moderately coarse, others exceedingly fine. *c.* a red blood-corpuscle with eccentric nucleus.

FIG. 45. (× about 1000). Human blood fibrin, to show the coarseness of the filaments and also centers of radiation. *c.* A red corpuscle drawn at the same scale.

FIG. 46. (× 700). Zoosperms of a lake lamprey. Three are shown entire. On each is a bulbous termination of the tail, and in the one at the right is an enlargement of the tail near the tip.

A. Two heads (× 2750). In the one at the right are shown two clear highly refractive bodies.

FIG. 47. Zoosperms of the sea lamprey. A single zoosperm drawn entire and magnified 700 diameters.

A. A head and the bulbous termination of the tail (× 2750.)

FIG. 48. Zoosperms of the brook lamprey. Two entire ones are shown at a magnification of 700. The tail of the one at the right is nearly uniform and ends in a point. The one at the left ends by a little knob as with the lake and sea lamprey.

A. Two heads magnified 2750 diameters.

FIG. 49. (Natural size). A glass vessel containing sand and water with a larval lamprey in its burrow, to show the position naturally assumed by the larvæ.

FIG. 50. (× 3). Head of a lake lamprey in the transforming stage to show the narrowed head and the snow white pineal eye.

1, 2. The first two branchiopores. *dc.* Posterior dorsal cartilage.

epi. Epiphysis or pineal eye surrounded by a light area.

n. Nostril with the opening directed obliquely cephalad

FIG. 51. Oblique view of the head and branchial region of an adult lamprey showing the direction of the expiratory currents from the branchiae and from the nasal sac.

bp. The branchiopores.

n. Nostril pointing obliquely cephalad.

so. Sensory organs, or nerve papillæ. Compare plates V and VI.

FIG. 52. (×4½). Frontal section, looking dorsad, of a larval lamprey, to show the velum and the course of the respired water.

1, 2, 3. Branchiopores covered with valves extending from the cephalic edge. *b, b, b, b,* Branchiae seen in section.

h. Hood or upper lip.

t. Oral tentacle. *v, v.* Velum. The two independent velar folds are shown in section.

vl. Valve over the branchiopore. In this one it is open for the passage of the expiratory stream, which is indicated as passing between the lamellæ of two contiguous gills.

The arrows show the stream entering the mouth through the straining tentacles, then between the two halves of the velum into the branchial chamber where it divides, part passing out between the gills of each side, and through the corresponding branchiopores.

FIG. 53, 54, 55. (×4½). Three views of the valves at the opening of the branchiopores that serve to direct the streams of water in inspiration and in expiration in the adult.

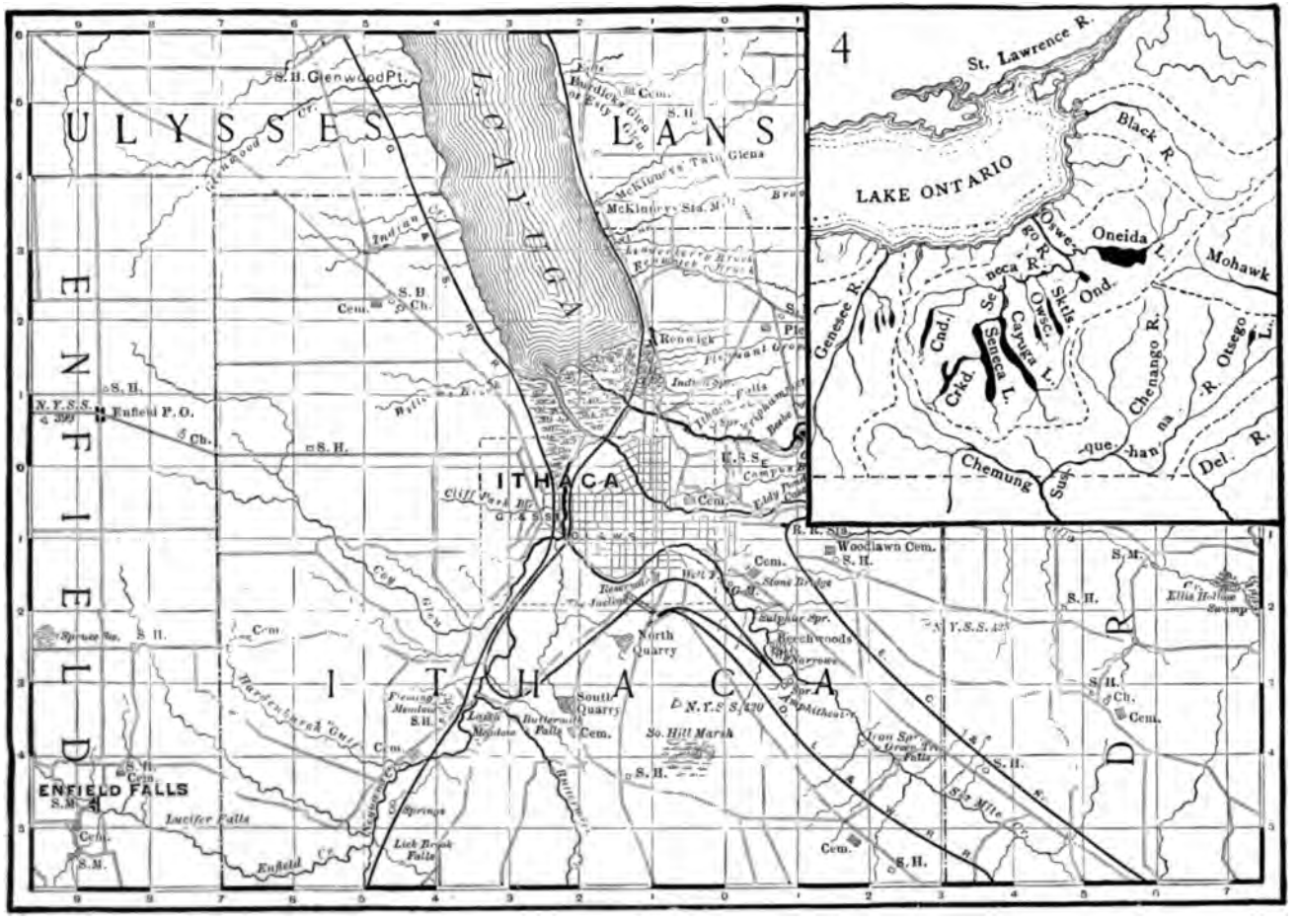
b, b. Branchiæ seen in section.

cl. Clavus or peg. A small, stiff, pointed body about 2 mm. high, arising on the caudal margin, and opposite the middle of the branchiopore. In expiration the two valves meet at this point, as shown in figure 55.

p. Fringe of papillæ on the caudal margin of the branchiopore. Their relation to the clavus is well shown in fig. 55.

vl. Valves. There are two, one extending dorso-ventrad as shown entire in fig. 55, and in section in fig. 53, 54. This one corresponds with the single valve of the larva.

The second, is a double valve within the branchiopore. In inspiration the two parts move up against the cephalic side of the branchiopore and are covered with the ectal or transverse valve and thus serve to guide the water directly into the gill sac. In expiration, fig. 54, 55, they rest against the caudal wall of the branchiopore, and, with the ectal transverse valve, make a tube directed obliquely caudad, thus giving a corresponding direction to the expiratory streams of water. See also fig. 51, 52.


ULYSSES
LANS
ENFIELD
ITHACA
ITHACA
DR
L. CAYUGA
S. H. Glenwood Pt.
Enfield P. O.
Renwick
Woodlawn Cem.
North Quarry
South Quarry
So. Hill Marsh
Beechwoods
ENFIELD FALLS
Lucifer Falls
Lick Brook Falls
Ellis Hollow Swamp
4
St. Lawrence R.
LAKE ONTARIO
Black R.
Oneida L.
Mohawk
Genesee R.
Oswego R.
Seneca R.
Ond.
Cnd.
Crkd.
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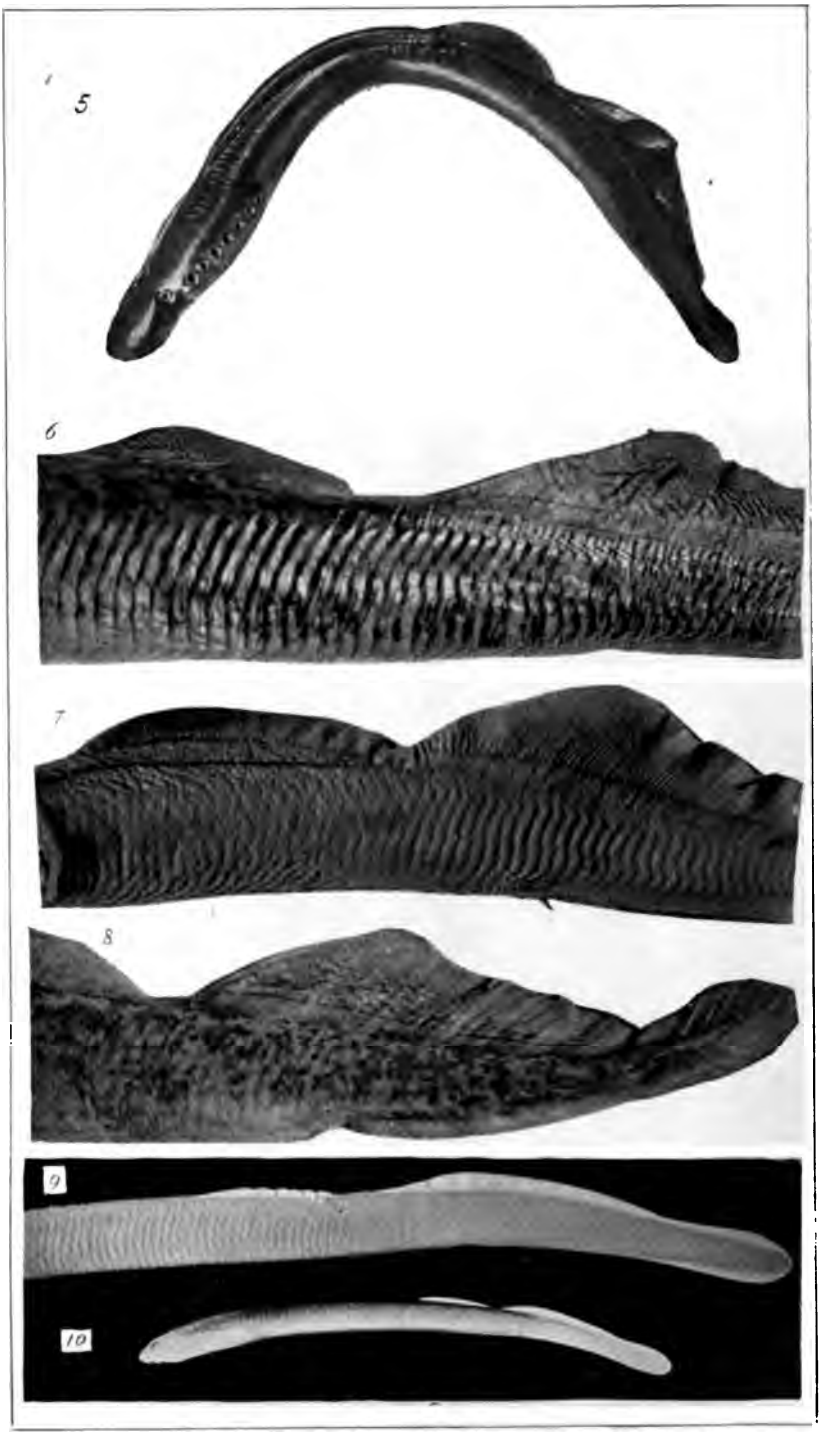
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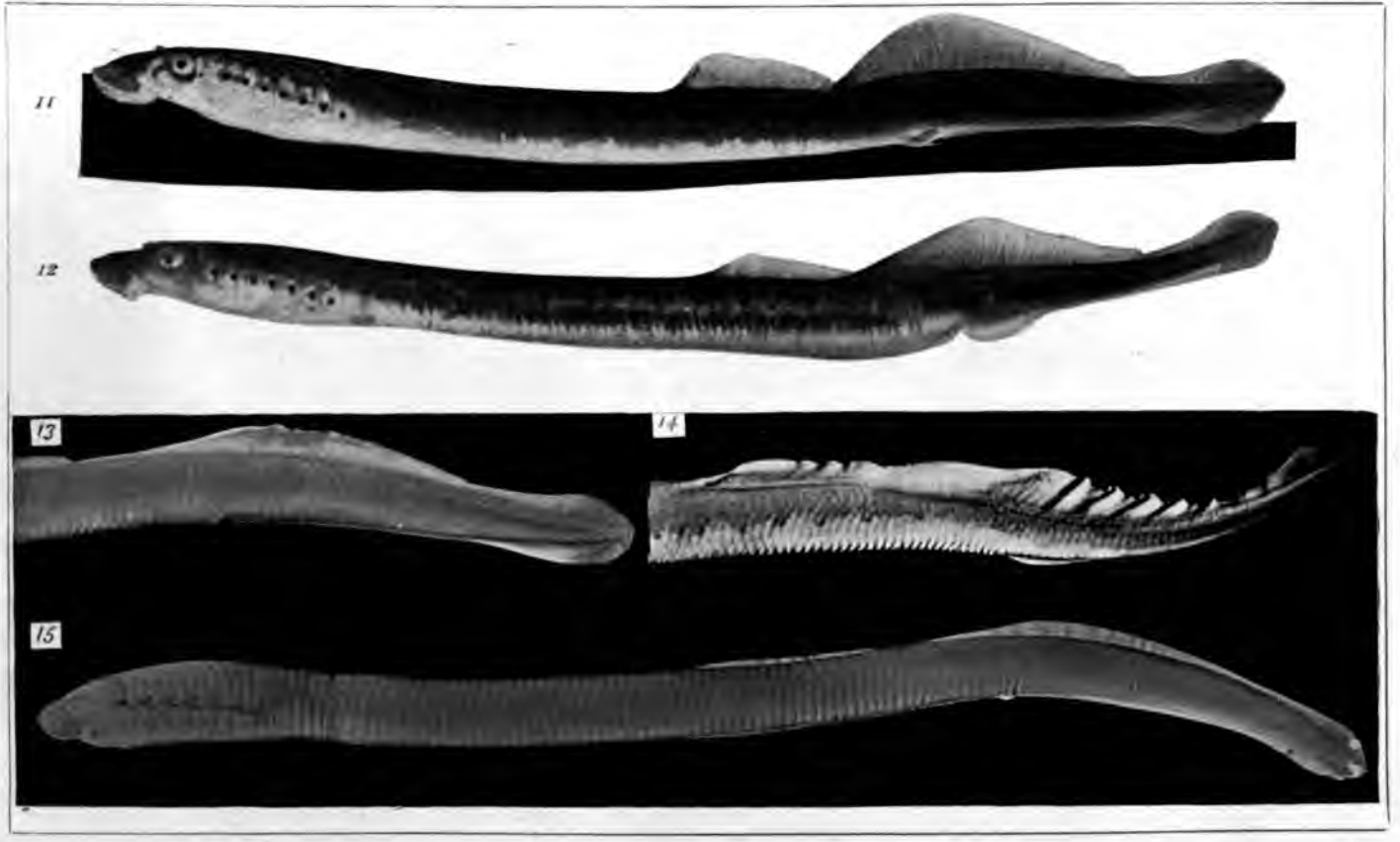
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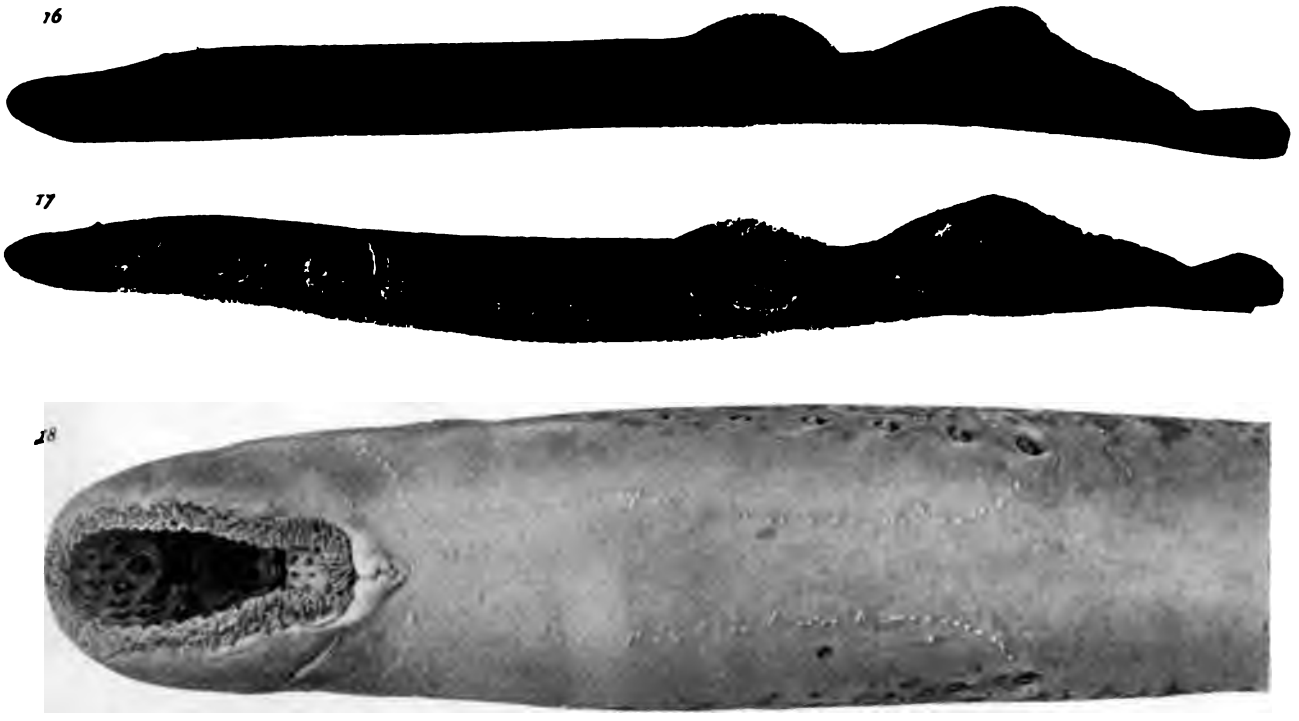
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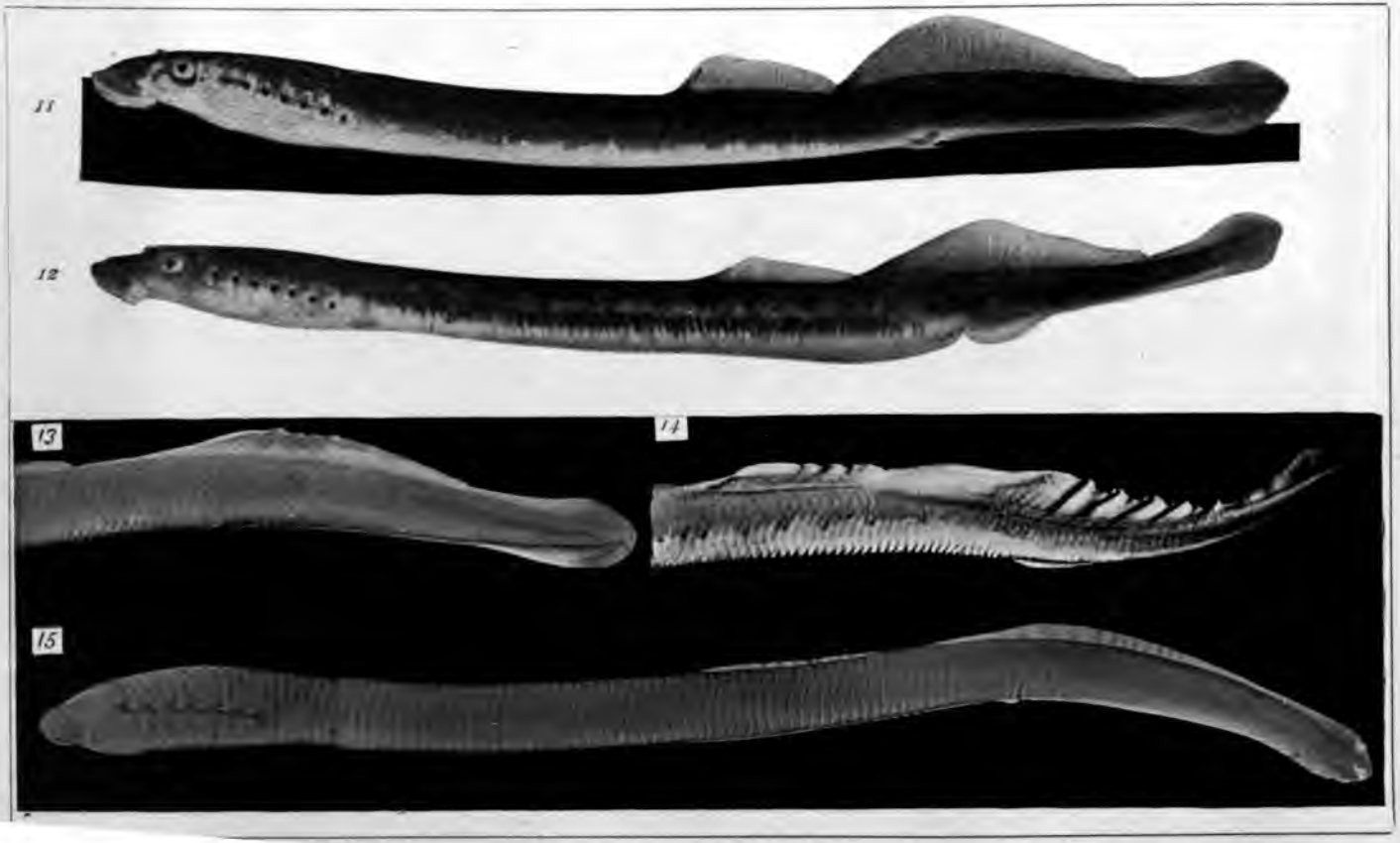
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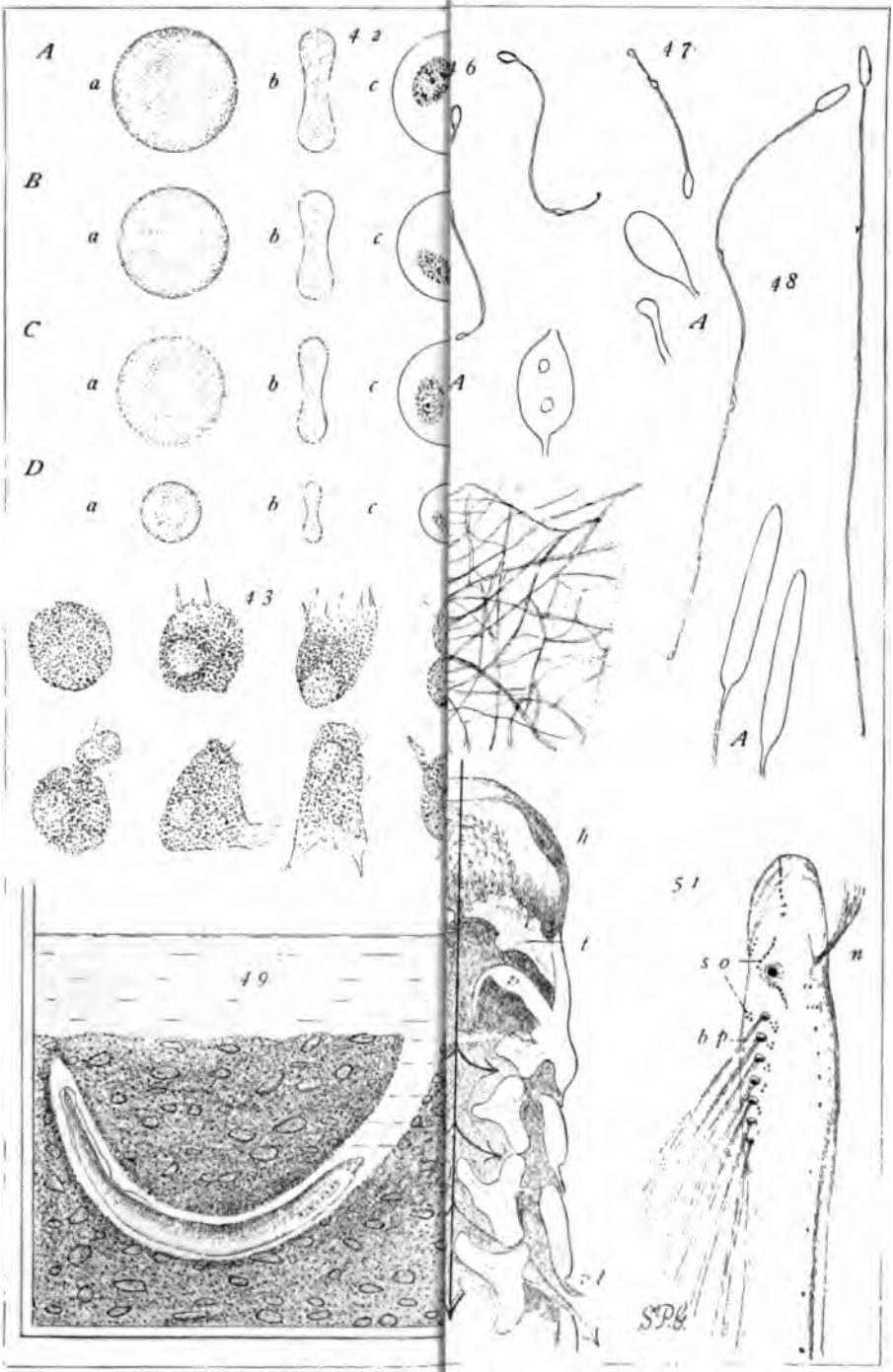
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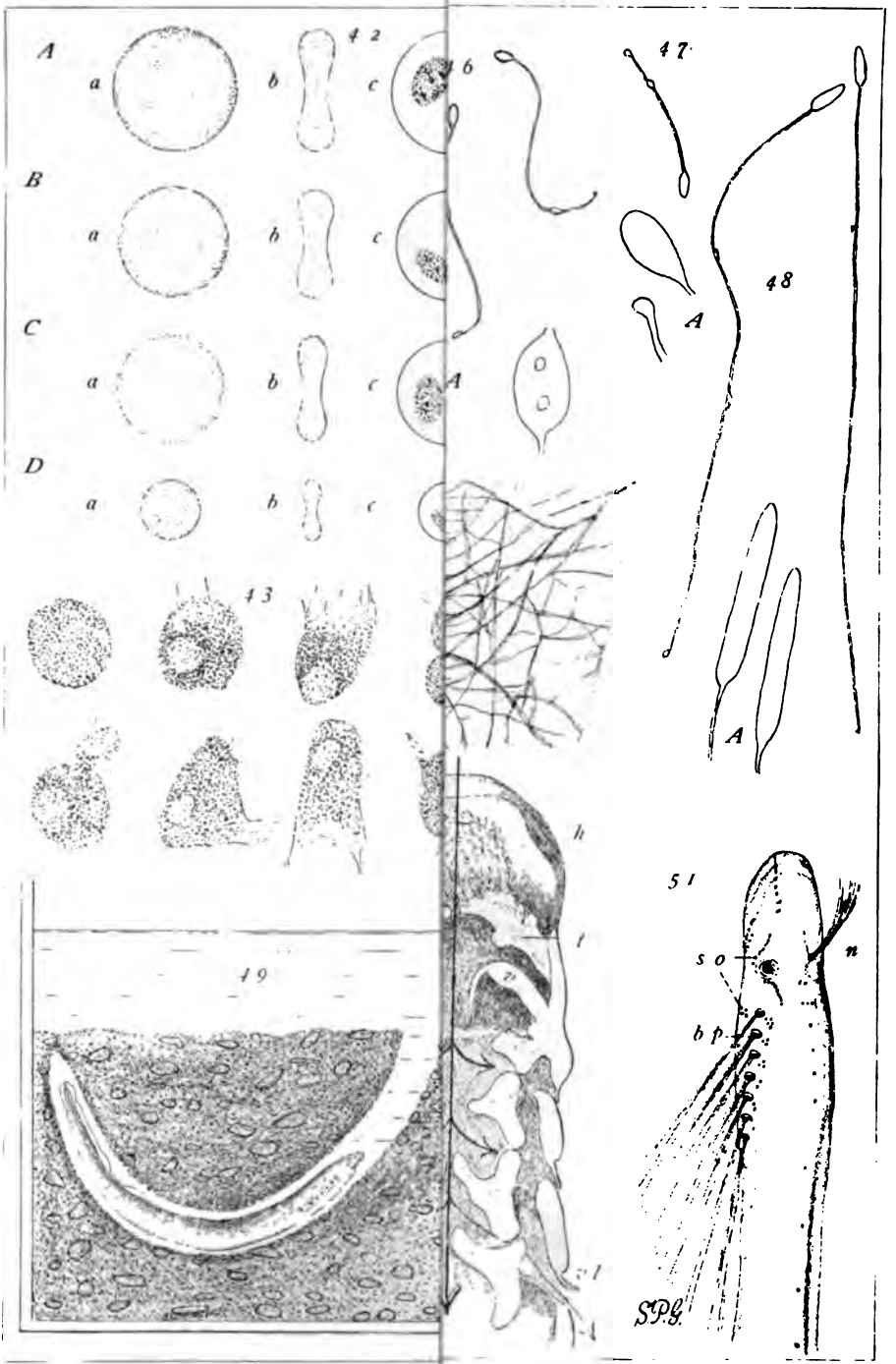
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